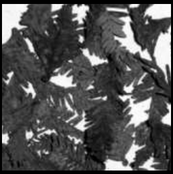

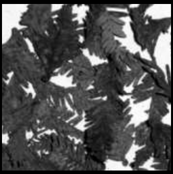


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The Geobiology and Ecology of *Metasequoia*

Edited by
Ben A. LePage, Christopher J. Williams and Hong Yang

Springer

THE GEOBIOLOGY AND ECOLOGY OF METASEQUOIA

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Trees of *Metasequoia glyptostroboides* growing along banks of the Yujiang River and base of the mountains in the Shiziba Valley, Hubei Province, China. Photography by Ben A. LePage, URS Corporation, Fort Washington, Pennsylvania.

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Contributors

This volume of the *Topics in Geobiology* series offers original contributions from the *1st International Metasequoia Symposium*, which was held on the campus of the China University of Geosciences in Wuhan, Hubei Province from August 5–7, 2002 and included a field trip to the native habitat of *Metasequoia*. The goal of this symposium was to provide an international forum where scientists who were actively involved in the study of fossil and living *Metasequoia* could unite to exchange ideas, assess the current state of knowledge and identify new research directions within a sound scientific framework. To this end, 51 participants from 4 countries were in attendance. The conference featured 21 contributed oral and 3 poster presentations. Presentations were organized around several themes: history and conservation of *Metasequoia*, paleobiology and ecology of *Metasequoia*, and modern ecology of *Metasequoia*. We are pleased that all of these themes are represented in the peer-reviewed contributions of this volume.

Renewed interest in the evolutionary history of *Metasequoia* indicated the need to establish a multi-disciplinary working group of scientists to initiate new and rigorous studies of this genus. This volume is an outgrowth of this working group. For scientists and the general public alike, few trees have fueled our curiosity and fascination, as have the redwoods for their size, longevity and their evolutionary history. Among the redwoods, *Metasequoia glyptostroboides* Hu *et* Cheng (Hu & Cheng, 1948) or the Dawn redwood, is probably one of the most interesting species, even though it is a more recent addition to the family. The dawn redwood was known initially only as a fossil and was first described in the scientific literature in 1941 by the Japanese paleobotanist, Shigeru Miki. Eight years later, the Chinese botanists Hu and Cheng unveiled a tree to the world that local residents of the Xiahoe Valley in southeast China called the Shui-Sha (Water Fir) and was morphologically identical to the fossils of *Metasequoia* that Miki had previously described.

Over the last 60 years, both the biology and paleobiology of the genus have been studied. Information regarding different features of the living species, ranging from morphology to genetics, has been accumulated. Hundreds of publications have appeared in which *Metasequoia* has been reported as a major or minor constituent of the fossil floras. Consequently, its fossil record is well known and indicates that the genus was widely distributed throughout the mid- and high-latitude regions of North America and Eurasia from early Late Cretaceous (ca. 100 million years ago) to Pliocene/Pleistocene time. The spatial and temporal distribution patterns indicate that *Metasequoia* was perhaps one of the most successful trees that occupied the temperate regions of the mid- and high-latitudes. At times *Metasequoia* was part of the broad-leaved temperate forests, while in others, large tracts of lowland swamp forests, consisting almost exclusively of *Metasequoia* are known to have existed, especially in the polar regions.

Today the genus has a distribution that is geographically restricted to two small disjunct regions in southeast China, with one of the two only represented by an isolated tree. Although *Metasequoia* was an important conifer throughout the mid- and high-latitudes forests of the Northern Hemisphere in the past, details of its modern ecological and physiological attributes are still poorly understood and scientific papers dealing with ecological aspects of the living representatives are few and often anecdotal. The primary objective of nearly all of the early expeditions led by western scientists to the native range of *Metasequoia* was to procure seeds and live plant material to prevent the extinction of this species. In contrast, there has been only limited study of *Metasequoia* ecology within its native habitat (e.g., Chu & Cooper, 1950). In fact, given its extensive fossil record we may know more about the paleoecology of *Metasequoia* than we do about the ecology of the extant species. With the construction of the Three Gorges Dam Project nearby, the habitat of living *Metasequoia* within the Xiahoe Valley may yet experience another dramatic change in the years to come. Thus, the need to compile known ecological information as well as documenting the existing status of the living species is urgent.

This book represents a distillation of the collective efforts and results of several *Metasequoia* specialists and enthusiasts. It is probably the most up-to-date and comprehensive reference source for the genus and the authors have sought to incorporate obscure, hard-to-get and non-English reference sources. The topics and scope of this book should be of interest to a wide audience including botanists, geologists, paleobotanists, biogeographers, foresters, ecologists, paleoecologists, ecophysiologists, geochemists, climate modelers, geneticists, naturalists, science historians, and not the least, gardeners. A brief summary of each contribution follows.

B.A. LePage, H. Yang and M. Matsumoto provide a comprehensive overview of the spatial and temporal distribution patterns of fossil *Metasequoia* in the Northern Hemisphere beginning in the early Late Cretaceous until the Pliocene-Pleistocene. The wide distribution of the genus indicates that it was capable of adapting and growing under a wide range of climatic and environmental conditions, including those unique to the polar latitudes. Although *Metasequoia* was a prominent constituent of the broad-leaved deciduous forests throughout the Northern Hemisphere, the genus appears to have been precluded from occupying Europe. Increasing global aridity, cooling and competition for space and resources from representatives of the Pinaceae appear to have contributed to the reduced distribution and abundance of the genus during the Neogene. The results of this study also indicate that with few exceptions, the genus has remained unchanged morphologically for 100 million years and provides another spectacular example of morphological stasis in the plant fossil record.

Recent stratigraphic and paleoenvironmental data have enabled A. Momohara to reconstruct the regional ecology and discuss the processes that led to the extinction of *Metasequoia* in Japan and its survival in China. A thorough evaluation of fossil *Metasequoia* in Japan and eastern Asia indicates that the genus was a common constituent in the wide sedimentary basins that were associated with contiguous fluvial flood plain ecosystems. Orogenic and volcanic activities in Japan influenced local topography in the adjoining or adjacent floodplains and may have influenced the distribution of *Metasequoia* during the mid-to late Neogene. The extinction of the last remaining populations of *Metasequoia* from Japan during the early Pleistocene and its re-appearance in China during the Holocene is discussed.

S.L. Richter and B.A. LePage present the results of a high-resolution palynological study on a siltstone unit located between two prominent coals representing *Metasequoia*-dominated swamp forests from the middle Eocene (ca. 45 million years old) Buchanan Lake Formation at Napartulik, Axel Heiberg Island, Nunavut, Canada. The pollen and spore microflora provides evidence of successional processes and indicates that the local vegetation responded to climatic and environmental changes. Furthermore, the pollen data indicate that the local floodplain vegetation was part of a larger, dynamic floral mosaic within a regional polar broad-leaved deciduous forest community and that periods of prolonged environmental stasis were generally limited to the swamp forest communities. Catastrophic flooding appears to have been a major disturbance factor throughout the landscape and fern spikes record at least two major flooding events.

H.W. Meyer examines the evolution of *Metasequoia* and the broad-leaved deciduous vegetation that became widespread in the Northern Hemisphere following the Eocene-Oligocene climatic cooling. He begins with an historical overview of Chaney's concepts of the composition and biogeographic history of North American fossil forests prior to and after the discovery of living *M. glyptostroboides* in China. Using the early Oligocene Bridge Creek flora of the John Day Formation in Oregon, USA as a model, Meyer suggests that the Mixed Mesophytic Forest originated through various responses of individual species during the Eocene-Oligocene transition, including 1) extinction or extirpation, 2) pre-adaptation or evolution in place, 3) dispersal from higher elevations, or 4) dispersal from higher latitudes.

J.B. Litoff recounts the story of how Wilhelm Gunther (1893–1983), a German national who lived and worked in China between 1914 and 1941, acquired seeds in the late 1920s that decades later would be identified as those of *M. glyptostroboides*. Drawing from historical and contemporary photographs as well as interviews with Gunther's daughters, this essay unravels the odyssey of these *M. glyptostroboides* seeds that possibly predate the discovery of the native population in China.

The discovery of Uneven and Even Type cuticle in native populations of *M. glyptostroboides* has prompted Q. Leng to conduct a re-evaluation of the taxonomic utility of cuticle characters in both living and fossil *Metasequoia*. The results of her study indicate that the Even Type cuticle appears to be restricted to a single tree located in Paomu Village, Hunan Province, China, whereas the Uneven Type cuticle is widely distributed in the main *M. glyptostroboides* populations. More importantly, all of the fossil *Metasequoia* leaves examined possess the Even Type, suggesting that the Even Type is the ancestral character state for the genus. This finding bears significant implications for the evolution and paleogeography of this genus, as well as the conservation of this endangered species.

K. Schoenhut examined mummified leaflets of middle Eocene *Metasequoia* from the Upper Coal member of the Buchanan Lake Formation at Napartulik on Axel Heiberg Island. She utilized transmission electron microscopy (TEM) to quantitatively and qualitatively assess the extent of sub-cellular preservation. The presence of organelles such as chloroplasts and chloroplast constituents were tallied on a per cross-section basis and by performing a nested multivariate analysis of variance, significant differences in leaf preservation were observed between individual leaflets as well as leaves between vertical intervals. Where discernible, thylakoid features were used to classify the fossil leaflets as originating from high or low-light environments. The results indicate that between 67 and 78% of the leaflets were classified as 'shade-types.'

Biomolecules from living and fossil *Metasequoia* have allowed H. Yang to provide insight into the biological and geological history of the genus, as well as its phylogeny and evolution, population genetics and molecular taphonomy. The chemistry of labile biomolecules and nucleotide sequences from

M. glyptostroboides reconfirm the systematic position of *Metasequoia* as the sister taxon to *Sequoia* Endlicher and *Sequoiadendron* J. Buchholz, which form the subfamily Sequoioideae. Relative rate testing based on different gene sequences suggests an evolutionary rate slow down in the Sequoioideae lineage, while non-sequence based studies indicate a low overall genetic diversity and a lack of spatial genetic structure in the native Chinese populations. Molecular and biochemical investigations of the ancient biomolecules from well-preserved Tertiary fossil *Metasequoia* remains reveal that labile biomolecules such as carbohydrates and cutin acids that are normally absent from the Cenozoic fossil record are preserved. Comparative geochemical and SEM analyses of these chemically unstable biomolecules and suggests that they may carry important structural functions to support the integrity of plant fossil morphology.

C.J. Williams provides a comprehensive update on the ecology and climatic conditions under which *M. glyptostroboides* grows in its native habitat in China as well as those growing in cultivation. The results indicate that the Chinese population grows under a narrow range of climatic and environmental conditions. The trees growing in cultivation however indicate that *M. glyptostroboides* is capable of growing across a gradient of 16.3°C of mean annual temperature and 2360 mm of mean annual precipitation. No cultivated *M. glyptostroboides* are known to exist without supplemental water in areas that receive less than ca. 500 mm of mean annual precipitation. Analysis of growth performance of *M. glyptostroboides* through time indicates that trees from different seedlots grown in common garden experiments remain static in their relative growth rates through time. A mixture of environmental factors may alter *M. glyptostroboides* growth form. Most notably, shrubby varieties are known from a mixture of cold climates, but are not always found in extremely cold areas.

D.R. Vann examines the modern species' autecology, focusing on gas exchange relations, to address the role of physiological constraints in range contraction over time. Examination of CO_2 uptake and transpiration in response to light, temperature, humidity and CO_2 concentration indicate that *M. glyptostroboides* is drought-intolerant, adapted to low light levels and relatively cool climates, as might be expected in foggy coastal or riparian habitats. Gas-exchange relations of the modern species are sufficiently flexible to explain the presence of fossil *Metasequoia* at all known sites and imply that the species has not undergone any major adaptive changes in its core physiological processes.

R. Jagels and M. Equiza examine the mechanical/hydraulic stem attributes, leaf-level water-use-efficiency and photobiology of *M. glyptostroboides, Sequoia sempervirens* (D. Don) Endlicher, *Taxodium distichum* (L.) Richard, *Glyptostrobus pensilis* (Staunton *ex* D. Don) K. Koch and *Larix laricina*

(Du Roi) K. Koch to consider the question of competitiveness of different tree species growing at the polar latitudes during the early Tertiary. The results indicate that *T. distichum* would have been limited primarily by a significant decrease in photosynthetic efficiency when growing under continuous light. *Sequoia sempervirens* should have been highly competitive, but was likely limited by its evergreen habit. *Glyptostrobus pensilis* would have been restricted to minor component status by its slow growth rate and short stature and although *L. laricina* demonstrated improved water-use-efficiency under continuous light, it had a less-competitive photobiology than *Metasequoia* and sequestered more resources into its stem biomass.

The Ryder's Lane Plantation at Rutgers University was established by J. Kuser after receiving a seedlot collection of *M. glyptostroboides* from China in 1990. In this paper Kuser provides an overview of the best method to propagate cuttings, hormone treatments and the best time of year to propagate cuttings of *M. glyptostroboides*. Furthermore, a brief discussion of three new cultivars awaiting introduction is provided.

C. Nugue provides a comprehensive overview of the known varieties of *M. glyptostroboides* that have either been described in the literature, are commercially available or in the process of being developed for commercial distribution.

G. Langlois presents a number of models that have been used previously for resource protection, including the program challenges and successes for the redwood forests in California, rainforests in Central and South America, coral reefs in Australia and the Giant panda in China. A Metasequoia Conservation Plan is discussed and tools for assessing the effectiveness of conservation programs are suggested.

It is our hope that through our continuing efforts and increased involvement of *Metasequoia* specialists and enthusiasts that the International *Metasequoia* Conference will convene again. By uniting *Metasequoia* researchers from across the globe and providing a forum for the dissemination of research findings the conference can contribute meaningfully to the ongoing conservation and research efforts focused on this unique species.

We would like to thank the contributors to this volume. Without their enthusiasm this volume would have never come to fruition. We would also like to extend our gratitude to the Chinese National Science Foundation, China University of Geosciences, Administration of Xingdoushan Natural Reserve, Andrew W. Mellon Foundation, Bryant College and Chinese Paleontological Association for funding. Thanks are due to the following manuscript reviewers for their helpful comments and suggestions: Pim van Bergen, David Cantrill, Geoffrey Creber, David Creech, Clyde Hunt, Steven Manchester, Thanh-Thuy Nguyen, Jon Parker, Dana Royer, Ken'ichi Saiki, Shinya Sugita and Catherine Yansa. Thanks are also due to Michael Leslie, Michael Leslie Photography for

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Ben A. LePage[1]
Christopher J. Williams
Hong Yang

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[1] We would also like to add that all royalties from this volume will be donated to the Xiaohe *Metasequoia* Conservation Station conservation fund so that basic, but much needed equipment can be purchased.

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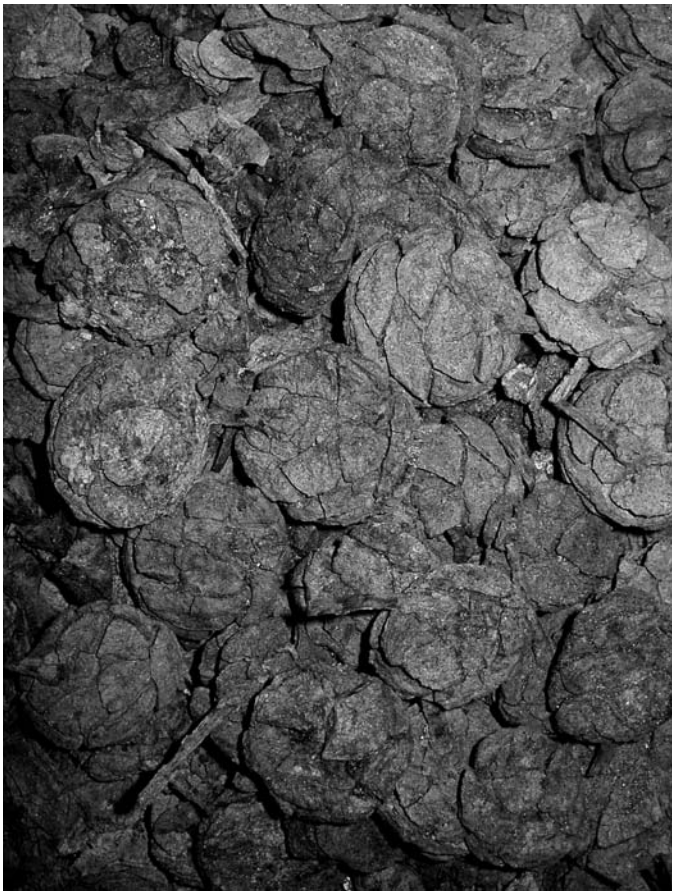
PART I

Fossil *Metasequoia* and History



Chapter 1

The Evolution and Biogeographic History of *Metasequoia*

BEN A. LePAGE[1], HONG YANG[2] and MIDORI MATSUMOTO[3]

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The Geobiology and Ecology of Metasequoia, edited by Ben A. LePage, Christopher J. Williams and Hong Yang,

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Abstract: The fossil record of *Metasequoia* Miki is extensive and demonstrates that the genus was widely distributed throughout North America and Eurasia from the early Late Cretaceous to the Plio-Pleistocene. The genus first appears in Cenomanian age deposits from western Canada, Alaska and the Arkagala and Koylma River basins in Russia and indicates that *Metasequoia* had achieved a wide distribution early in its evolutionary history. Exchange of *Metasequoia* between Asia and North America probably occurred across Beringia, which had become functional at the Albian-Cenomanian boundary (ca. 100 million years ago). However, if the inter-continental exchange of the early representatives of this genus occurred prior to the establishment of Beringia, migration would have still been possible across the Spitsbergen Corridor, which was functional during the Early Cretaceous. By the early Tertiary, the distribution patterns do not appear to have changed considerably from that seen during the Late Cretaceous, except that *Metasequoia* became a dominant constituent of the polar Broad-leaved Deciduous Forests. More importantly, the distribution of *Metasequoia* indicates that the genus grew and reproduced under a diverse range of climatic and environmental conditions throughout geologic time, including the cold and unique lighting conditions of the polar latitudes. Of particular interest is the apparent lack of *Metasequoia* fossils in Europe despite the presence of two land bridges linking North America and Europe throughout the early Tertiary and the drying of the Turgai Straits that separated eastern and western Asia up until Oligocene time. *Metasequoia* persisted in western Siberia and the Canadian Arctic until late Pliocene time, and in western Georgia and Japan until the late Pliocene-early Pleistocene. Following the apparent early Pleistocene extinction, *Metasequoia* re-appeared in southeastern China. The pronounced reduction in distribution during the Miocene appears to be coupled with increasing global aridity and cooling and increased competition for resources and habitat from representatives of the Pinaceae. With few exceptions, the bulk of the *Metasequoia* fossils described in the literature indicate that the fossils assigned to *M. occidentalis* are indistinguishable from the living species. The remarkable morphological stasis observed in *Metasequoia* demonstrates that the genus has remained unchanged, at least morphologically, since the early Late Cretaceous.

Key words: China; Cretaceous; evolution; mycorrhiza; land bridges; Napartulik; orogeny; paleogeography; Shui-sha-ba Valley; systematics; taxonomy; Tertiary; Turgai Stait.

1. INTRODUCTION

Metasequoia Miki (Miki, 1941) is one of seven monospecific genera within the Taxodiaceae (now subsumed within the Cupressaceae), with *Metasequoia glyptostroboides* Hu *et* Cheng (Hu & Cheng, 1948) occurring in small and possibly relictual populations in Sichuan, Hubei and Hunan Provinces, China. It occurs as a constituent of the mixed mesophytic forests and grows at elevations ranging from 800 to 1,500 m (Fu & Jin, 1992). *Metasequoia glyptostroboides* grows on acidic alluvial soils in the mountain valleys where there is abundant moisture, mean annual temperature (MAT) is about 13°C, the coldest month mean temperature ranges from –6.1 to 1.7°C (absolute coldest –15.4°C) and the warmest month mean temperature ranges from 23.3 to 32.3°C (absolute warmest 35.4°C) (Bartholomew *et al.*, 1983; Fu & Jin, 1992). Rainfall is seasonal with a mean annual precipitation of about 1,300 mm (climate data from Lichuan [1959–1978]); Wang, 1961; Bartholomew *et al.*, 1983; Fu & Jin, 1992). For a detailed discussion on the ecology and environment of *M. glyptostroboides* see Williams (this volume).

Although *M. glyptostroboides* currently grows in a part of the world that is moderately warm, it must be pointed out that the temperature conditions under which *M. glyptostroboides* grows today should probably not be considered indicative of the temperatures or environmental conditions under which the ancient representatives of the genus grew, or that *M. glyptostroboides* is incapable of growing under much colder conditions. Snow and freezing temperatures were reported to occur regularly during the winter months by local residents of Modaoxi (Modaoqi), which is located within the Shui-sha-ba (Chinese for *Metasequoia*) Valley where *M. glyptostroboides* is thought to occur naturally (LePage, personal communication with local residents, 2002). *Metasequoia glyptostroboides* trees growing in Montreal, Canada and St. Petersburg, Russia frequently experience winter temperatures as low as –30°C to –40°C (Williams, this volume; LePage, unpublished) and laboratory experiments have shown that the leaves and twigs are frost resistant to temperatures as low as –30°C (Sakai & Larcher, 1987). Wang (1961) indicates that the genus probably had a much more extensive distribution during Recent time and grew under a wider range of environmental conditions than that indicated by the modern, geographically restricted, native populations.

The occurrence of fertile and vegetative remains of *Metasequoia* in the plant fossil record indicates that the genus possessed a much wider distribution that extended well into the polar regions of the Northern Hemisphere throughout the Mesozoic and Cenozoic (Figure 1-1; Appendix A; Florin, 1963; Yang, 1999, Yang & Jin, 2000). Moreover, such a wide distribution in space and in time indicates that representatives of the genus probably grew under a diverse range of climatic and environmental conditions throughout geologic time. The lack of significant morphological diversification observed between living and fossil *Metasequoia* foliage and seed cones leaves little doubt of the accuracy of the fossil identifications. In fact, in almost every report where *Metasequoia* fossils have been described, the authors point out that they are more or less identical to living *M. glyptostroboides*. Nevertheless, the practice of erecting new names for fossil species of *Metasequoia* based on slight differences in the size and shape of the fossil remains, or geologic age has, and continues to pervade the literature.

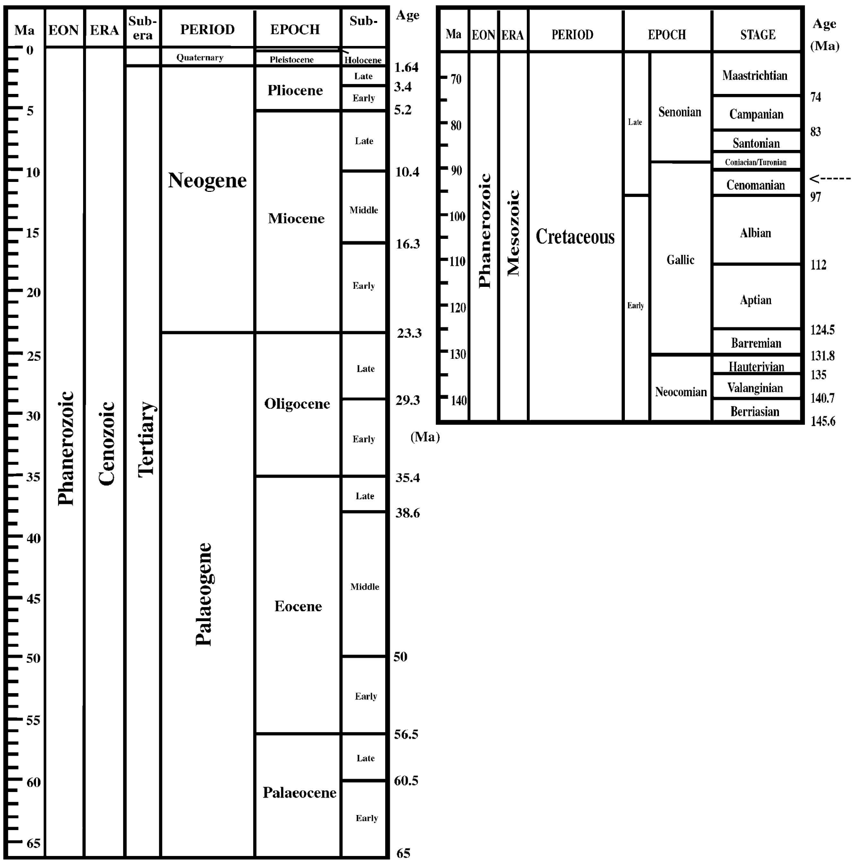

Figure 1-1. Mesozoic and Cenozoic chronostratigraphic chart. Redrawn and modified from Taylor and Taylor (1993). Arrow at the Cenomanian indicates the first occurrence of fossil *Metasequoia* from Russia, Canada and Alaska.

In this paper, the evolution and biogeographic history of the genus are discussed in light of the tectonic and climatic history of the Northern Hemisphere. Examination of the fossils reported in the literature indicate that most of the fossils conform morphologically to the living species *M. glyptostroboides*, providing a spectacular example of morphological, and possibly genetic stasis over a geologically-long period of time.

2. TAXONOMY

The affiliation of *M. glyptostroboides* with the Taxodiaceae was clearly established in the initial description of the fossil material (Miki, 1941) and was substantiated by later studies using living specimens (Hu & Cheng, 1948). Shortly after the living trees were discovered in China, Stebbins (1948) performed the first chromosomal analysis. His work along with studies by Schlarbaum *et al.* (1983, 1984) indicated that *M. glyptostroboides*, ($2n = 22$) is closely related to *Sequoiadendron* J. Buchholz ($2n = 22$) and *Sequoia* Endlicher ($2n = 66$; Figure 1-2). Further molecular studies on the phylogeny of the genus using proteins and nucleotide sequences re-affirmed this grouping and further pointed out that the three taxa formed a "redwood clade (or sequoiod clade)" (Price & Lowenstein, 1989; Brunsfeld *et al.*, 1994). This phylogenetic placement was further supported by recent PCR-RFLP data (Tsumura *et al.*, 1995) and multi-gene analyses (Kusumi *et al.*, 2000) (for details see Yang, this volume). Combining the molecular and morphological data, Gadek *et al.* (2000) adopted earlier suggestions (Pilger, 1926; Eckenwalder, 1976; Brunsfeld *et al.*, 1994) that recognized elevation of these three genera to the intra-familial level, the Sequoioideae, within the family Cupressaceae (Figure 1-2).

Metasequoia is one of the most abundant and easily recognized plant fossils found in the Late Cretaceous and Tertiary fossil plant record of the Northern Hemisphere (Chaney, 1951; Florin, 1963; Liu *et al.*, 1999; Yang, 1999; Yang & Jin, 2000). Prior to the discovery and description of fossil *Metasequoia* from the late Miocene and Pliocene of Japan (Miki, 1941; Momohara, this volume), most *Metasequoia* remains, commonly seed cones and leaves, were assigned to *Glyptostrobus* Endlicher, *Sequoia*, *Taxites* Brongniart or *Taxodium* Richard (Appendix A). In his seminal paper, Chaney (1951) provided the most up-to-date account of fossil *Metasequoia* in North America. He recognized two fossil species that corresponded to different geologic ages and assigned fossil *Metasequoia* remains from Cretaceous deposits to *M. cuneata* (Newberry) Chaney and those from the Tertiary to *M. occidentalis* (Newberry) Chaney.

Following the establishment of the fossil genus *Metasequoia* more than 20 names for extinct species of the genus were erected over the next 60 years (Liu *et al.*, 1999, Appendix A). Recently, Liu *et al.* (1999) found that almost all of these species were based on slight differences in the size and shape of the leaves and seed cones, and that the morphological variation of the fossil remains seen among these 20+ species was part of the natural morphological variability inherent to *M. occidentalis*. Liu *et al.'s* (1999) morphometric analyses led them to conclude that only two species of fossil *Metasequoia*, *M. occidentalis* and *M. milleri* Rothwell *et* Basinger could be recognized from the entirety of the fossil record of the genus. More recently, Stockey *et al.* (2001) recognized a third species, *M. foxii* Stockey, Rothwell *et* Falder from Paleocene (late Tiffanian [Ti_4]) Paskapoo Formation, Alberta, Canada. The establishment of this new species was based on the examination of more than 10,000 specimens.

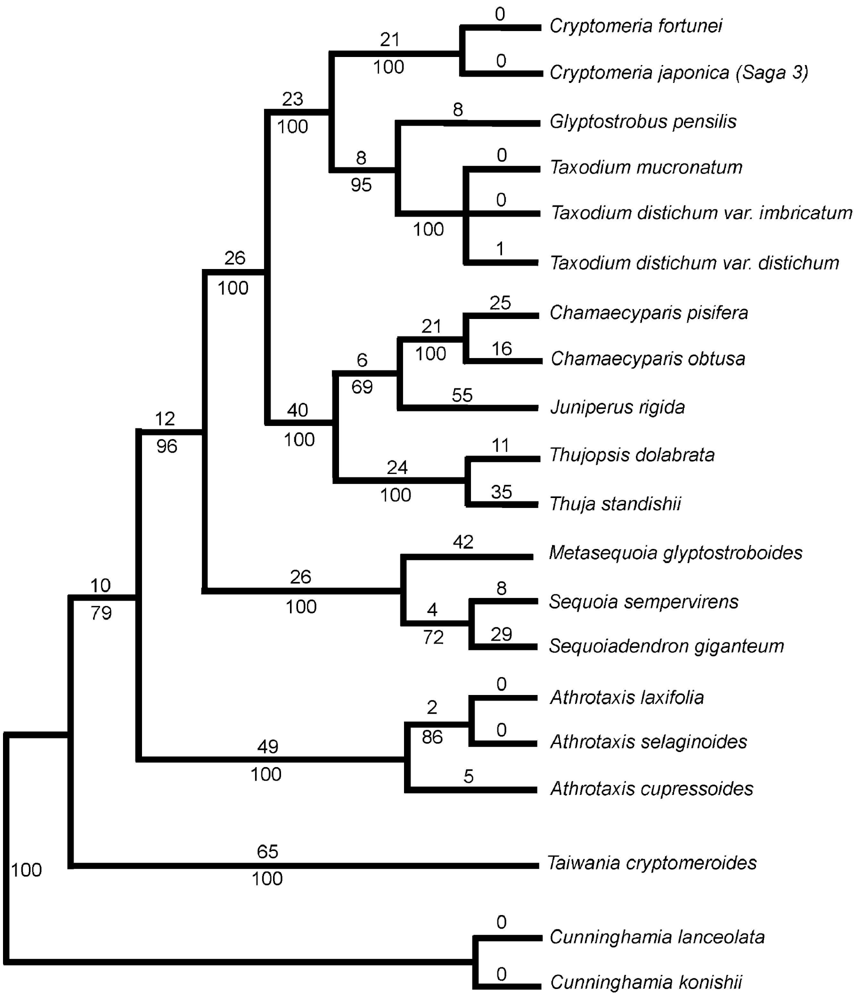

Figure 1-2. Most parsimonious tree for genera of the Taxodiaceae and Cupressaceae *s.s.* by the maximum parsimony method based on sequences of the *matK* gene, *chlL* gene, *trnL-trnF* IGS region and trn intron. The number above each branch is the number of steps separating each node and the numbers below indicate the percent of bootstrap values estimated from 1000 bootstrap replicates. The tree is rooted with *Cunninghamia*. Tree length = 645; Consistency index = 0.860; Retention index = 0.908. Redrawn and modified from Kusumi *et al.* (2000).

3. MORPHOLOGICAL STASIS AND GENETIC VARIATION

The lack of considerable morphological variability and species diversity seen in the fossil record of *Metasequoia* since its appearance in the Late Cretaceous is important. The longevity of biological species is estimated to be less than 10 million (Ma) years and presumed to be the same for all taxa (Raup, 1986). Niklas *et al.* (1983) suggested that the longevity of fossil angiosperms was 3.5 million years. Although there are no data specific to the gymnosperms. Most species gymnosperms are arborescent and the time from germination to sexual maturity is considerably longer then most engiosperms. Therefore species longevity of the gymnosperms is likely between 3.5 and 10 million years. Nevertheless, species longevity within some of the homosporous filicalean ferns and certain conifers, including *Metasequoia*, depart from the proposed extinction pattern by up to an order of magnitude (Rothwell & Stockey, 1991; LePage & Basinger, 1995; Serbet & Rothwell, 2000, Stockey *et al.*, 2001). However, the mechanism(s) responsible for such prolonged morphological stasis are still poorly understood.

There is evidence that indicates that the rates of morphological and molecular evolution are correlated and that there is a wide range of rate heterogeneity among taxa that have been examined, but none of these studies included conifers in their analyses (Omland, 1997; Barraclough & Savolainen, 2001). It has also been noted that karyotypic evolution in the gymnosperms is significantly slower than the rates of change seen in amino-acid sequences (Wilson *et al.*, 1974a, 1974b; Praeger, 1976; Niklas *et al.*, 1985). Omland (1997) suggested that the frequency of species bottlenecks and founder events might either accelerate or slow morphological and molecular evolutionary rates. If the rates of morphological and molecular evolution were correlated, the lack of morphological variability seen in taxa such as *M. glyptostroboides* would predict that the rate of molecular evolution is also low. (Yang, this volume). However, the allozyme variation of 46 single-tree seedlots of *M. glyptostroboides* seeds collected from Hubei and Sichuan Provinces in 1990 and planted at the Ryder's Lane Plantation at Rutgers University in New Brunswick, New Jersey indicate that the genetic diversity of *M. glyptostroboides* is low to average compared to other conifers, with high measures of inbreeding and genetic differentiation (Kuser *et al.*, 1997, this volume).

Metasequoia foxii is known only from two localities in Alberta, while *M. milleri* is known only from the middle Eocene Allenby Formation of south central British Columbia, Canada. With the exception of *M. foxii* and *M. milleri*, the morphological stasis observed in *M. occidentalis* is truly remarkable. Despite the fact that *M. occidentalis* was so widely distributed throughout the Northern Hemisphere for nearly 100 Ma and grew as a pioneer species under a wide range of climatic and environmental conditions, detailed examination of the gross morphological features indicates that the morphology of the genus has remained unchanged since it first appeared during Cenomanian time. However, as pointed out by Stockey *et al.* (2001) it is unlikely that the genus was comprised of only three species throughout its evolutionary history and that more species may remain yet to be discovered. The recognition of at least twenty horticultural varieties of *M. glyptostroboides* indicates that the living species is capable of producing distinct morphotypes that could potentially evolve into new species (Kuser, this volume; Leng, this volume; Nugue, this volume).

4. DISTRIBUTION OF *METASEQUOIA GLYPTOSTROBOIDES*

Today the genus is restricted to an area of approximately 800 km^2 along the border of Sichuan, Hunan and Hubei Provinces, China. As recently as 1950 there is evidence to suggest that the distribution of *M. glyptostroboides* in China may not have always been restricted to the presently known locations (Qi *et al.*, 1993; Litoff, this volume). However, these claims await further support from field surveys. The main population occurs in a 25 km long and 1.5 km wide strip along the Modao River in the Shui-sha-ba Valley, Zhonglu Town, Lichuan County, Hubei Province at elevations ranging from 900–1250 m. In the Shui-sha-ba Valley natural stands of *M. glyptostroboides* are comprised of 30–40 individuals and can be found growing on the sides of hills and ravines where moisture is abundant. Those growing on the valley floor and along rivers are thought to have been planted (Figure 1-3; Chu & Cooper, 1950; Meyer, this volume, Williams, this volume).

Figure 1-3. A small grove of *M. glyptostroboides* that appear to have been planted along the bank of the Yujiang River near Shiziba, China.

A second and potentially important tree was recently discovered in Paomu near Luota Town in the Longshan area of Hunan Province. Although the *M. glyptostroboides* tree from this area is architechturally and morphologically indistinct from those of the Shui-sha-ba Valley, micromorphological features of the cuticle indicate that the leaves of the Paomu tree are distinct from those of the Shui-sha-ba Valley populations. More importantly though, Leng *et al.* (2001) and Leng (this volume) compared the anatomy of fossil *Metasequoia* cuticle to the Shui-sha-ba Valley populations and the Paomu tree and found that in every case, the fossil cuticle resembled that of the Paomu tree. Clearly the importance of this discovery and the Paomu tree cannot be emphsized enough if we are to better understand the evolutionary history of the genus. Although there are other reports of *M. glyptostroboides* from other remote areas in Hunan and Sichuan Provinces (see Ling, 1976), a recent field survey has confirmed the Sichuan distributions and two sites in Human Province (H. Yang and Q. Leng, personal observations).

5. PHYTOGEOGRAPHY

The fossil record of *Metasequoia* indicates that the genus was widely distributed throughout the Northern Hemisphere from the Late Cretaceous until the Plio-Pleistocene (Figures 1-4 to 1-12; Appendix B; Florin, 1963; Yang, 1999; Yang & Jin, 2000). However, the fragmentary nature of many of these fossils, along with incomplete descriptions and poor illustrations provided in the literature has made phylogenetic interpretation of fossil *Metasequoia* difficult. *Metasequoia foxii* and *M. milleri* were established on anatomical differences and as Stockey *et al.* (2001) concluded, there is no reason why the genus should only be comprised of three species over its entire evolutionary history. Although species segregation using gross morphological features appears to provide little useful phylogenetic information, we expect that further detailed anatomical studies on currently known and new fossil *Metasequoia* remains may ultimately reveal that the genus possessed a rich and speciose fossil history. As such, the synonomy of fossil *Metasequoia* that we have compiled in Appendix A is based on a detailed literature review and will likely require revision as future taxonomic studies are undertaken. We have made no attempt to revise the current taxonomy of *Metasequoia* as this effort was outside of the scope of this paper.

Nevertheless, the totality of these fossils is important for understanding and interpreting the biogeographic history of the genus. The difficulties associated with providing a reliable and meaningful assessment of the number of species throughout the fossil record of the genus limits the usefulness of interpreting the biogeographic history of the genus at the species level. Therefore, the biogeographic history of the genus is best viewed as being that of a single entity.

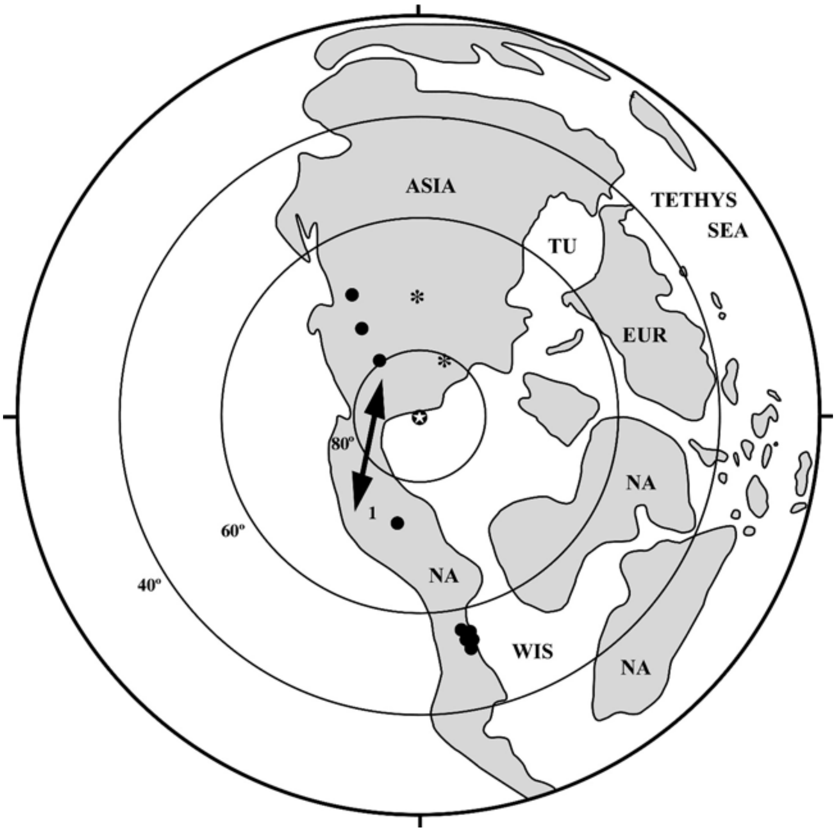

Figure 1-4. Generalized paleogeographic reconstruction of the Northern Hemisphere in polar projection during the early Late Cretaceous (Turonian, ca. 92 Ma), showing the Beringian Corridor (1) and the distribution of fossil *Metasequoia. Legend:* NA = North America, WIS = Western Interior Seaway, EUR = Eurasia; TU = Turgai Strait; ● = Cenomanian; and * = Turonian. Figures 1-4 to 1-9 are modified after LePage & Basinger (1995a) and the references therein.

Prior to discussing the phytogeographic history of *Metasequoia*, a number of points need to be iterated. Although it is tempting to suggest that the earliest occurrences represent a point of origin, we must remember that the plant fossil record, or any fossil record for that matter, is fragmentary and provides only the briefest of glimpses into a plant's evolutionary history. The use of the plant fossil record to interpret the phytogeographic history of a taxon such as *Metasequoia* represents an interpretation that is based ultimately on a partial data set only. Therefore, the lack of data from a region does not necessarily mean that the genus did not occur there (however, one would not expect a boreal or temperate species to be growing in the sub-tropical/tropical regions). Some possibilities that might explain the lack of *Metasequoia* fossils from a region include:

(1) the chance entry of its remains into the appropriate depositional environment did not occur; (2) the plants entered the appropriate depositional environment, but were not preserved; (3) we have not yet found fossils of that taxon; (4) the fossils may not be recognisable as being those of *Metasequoia*; or (5) the deposits that may have contained *Metasequoia* fossils were destroyed given the glacial history of the Northern Hemisphere. Consequently, as more or new data become available, the original biogeographic interpretations can either become more robust or new patterns can be recognised.

Metasequoia is first recorded in the Cenomanian Arkagala Formation from the Arkagala River and Kolyma Rivers, Russia, the Amkinskaya Formation from the Okhotsk-Chukotka Volcanogenic Belt in the Ul'inskiy Trough near Amka, Russia, unnamed Cenomanian deposits along the Yukon River in Alaska and the Cenomanian Dunvegan Formation from western Canada (Figure 1-4; Appendix A; Hollick, 1930; Baikovskaya, 1956; Samylina, 1962, 1964; Bell, 1963; Lebedev, 1976, 1979, 1982, 1987; Patton & Moll-Stalcup, 2000). The Russian localities were located between about 70°N to 80°N, while those in western Canada and Alaska ranged from around 55°N to over 70°N. Although the most southern locations in Russia and Canada were separated by thousands of miles, biotic interchange between Asia and North America probably occurred via the Beringian Corridor, which was established by Albian time (ca. 100 Ma). However, if the genus possessed a significant Early Cretaceous history that has either not been recorded as part of the fossil record or not yet recognised, the establishment of these apparently disjunct populations would have likely occurred via the Spitsbergen Corridor (LePage & Basinger, 1995).

Regardless of the migrations routes used by *Metasequoia*, the data at hand indicate that (1) *Metasequoia* appears to have had an Early Cretaceous origin, (2) *Metasequoia* was a constituent of the broad-leaved deciduous forests in the polar regions early in its evolutionary history, which may have important implications in the evolution of deciduousness (Vann, this volume) and (3) migration between North America and Asia occurred through the Beringian Corridor, and possibly through the Spitsbergen Corridor if intercontinental migration occurred prior to the establishment of the Beringian Corridor. Further paleobotanical research on Early Cretaceous deposits from Alaska and Chukotka may ultimately provide answers to some of these questions.

The early Late Cretaceous (Cenomanian and Turonian) distribution pattern of *Metasequoia* shown in Figure 1-4 also illustrates two important points. The first is that the genus grew at latitudes ranging from approximately 55°N to over 80°N and experienced a wide range of climatic and environmental conditions. Its polar distribution is particularly interesting because data indicate that *Metasequoia* occurred well above the Arctic Circle and would have grown under the unique polar light regime. That is, the trees would have experienced 3 months of continuous light in summer and 3 months of total darkness during the winter. If we assume that the genus was deciduous, as is the case today, it would have then been well positioned to thrive in these unique polar environments. Second, there is a growing body of evidence to support the idea that the polar regions were cold with freezing temperatures during the dark winter months throughout the Cretaceous and early Tertiary (see LePage, 2003b and references therein). This indicates that the genus was able to tolerate a wide range of temperatures early in its evolutionary history with little effect on its gross morphological features and contradicts the notion that *Metasequoia* cannot tolerate cold or freezing conditions.

By the Late Cretaceous (Coniacian, Santonian, Campanian and Maastrichtian [=Senonian]) the genus was well established along the western coast of North America and the eastern coast of Asia (Figure 1-5). The latitudinal range of distribution extended from about 30°N to about 70°N.

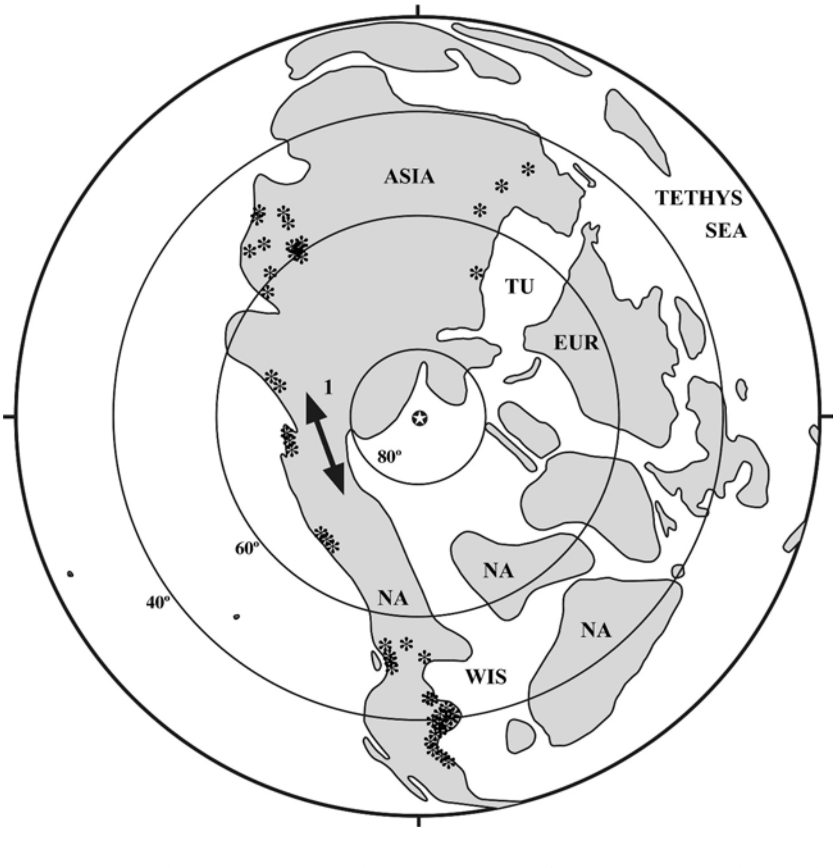

Figure 1-5. Generalized paleogeographic reconstruction of the Northern Hemisphere in polar projection during the Late Cretaceous (Maastrichtian, ca. 71 Ma), showing the Beringian Corridor (1) and the distribution of fossil *Metasequoia*. *Legend:* NA = North America, WIS = Western Interior Seaway, EUR = Eurasia and TU = Turgai Strait.

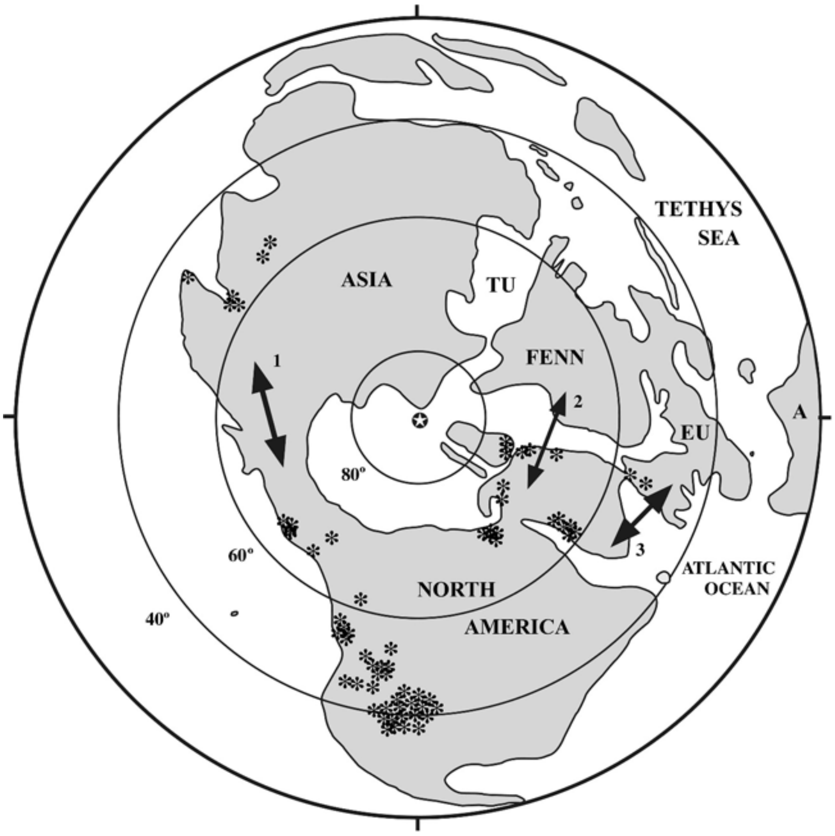

Figure 1-6. Generalized paleogeographic reconstruction of the Northern Hemisphere in polar projection during the Paleocene (ca. 60 Ma), showing the Beringian Corridor (1), DeGeer Route (2), Thulian Route (2) and the distribution of fossil *Metasequoia.* Note the spread of *Metasequoia.* into the westernmost part of Eurasia. *Legend:* TU = Turgai Strait, EU = Europe, A = Africa and FENN = Fennoscandia.

However, at this time the genus showed signs of range expansion into western Asia up to the shores of the Turgai Strait. Maastrichtian age floras from eastern Kazakhstan and the Kuznets Basin indicate that the climate was cooling and becoming more mesic (Baikovskaya, 1956; Makulbekov, 1974; Shilin & Romanova, 1978; Vakhrameev, 1988).

By the early Tertiary, three land bridges were available to flora and fauna for exchange between Asia, North America and Europe (Figures 1-6 and 1-7). The DeGeer Route (McKenna, 1972a, 1983a) linked North America and Fennoscandia throughout the Paleocene and Eocene, while the more southern Thulian Route existed intermittently or as a series of islands between southern Greenland and Europe, also during Paleocene and Eocene time (McKenna,

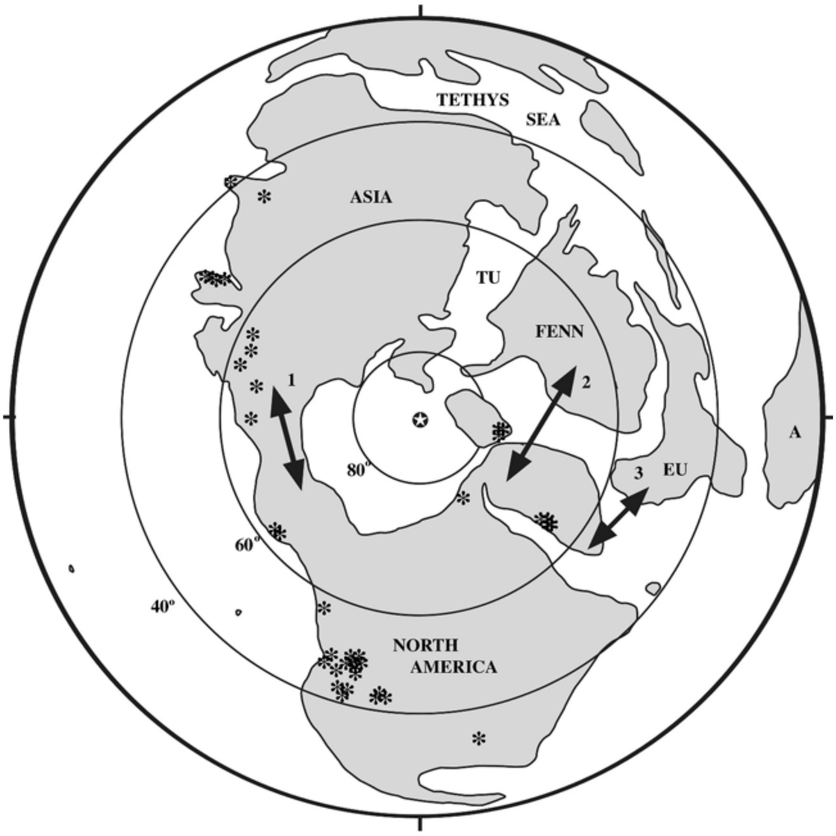

Figure 1-7. Generalized paleogeographic reconstruction of the Northern Hemisphere in polar projection during the middle Eocene (ca. 45 Ma), showing the Beringian Corridor (1), DeGeer Route (2), Thulian Route (3) and the distribution of fossil *Metasequoia.* By the end of the Eocene, the DeGeer and Thulian routes between North America and Europe had been broken. *Legend:* TU = Turgai Strait, EU = Europe, A = Africa and FENN = Fennoscandia.

1972a, 1975; Thiede & Eldholm, 1983). The Beringian Corridor remained a functional conduit between North America and Asia until Pleistocene time (Chaney, 1947; Hopkins, 1967; McKenna, 1972a; Tiffney, 1985).

The early Tertiary (Paleocene and Eocene) distribution pattern of *Metasequoia* indicates continued occupation of western North America and eastern Asia (Figures 1-6 and 1-7). The distribution of the genus in North America appears to have experienced considerable range expansion in the foreland and inter-montane basins of the rising Rocky Mountain Range. In the polar regions, *Metasequoia* became a prominent component of the Greenland, Spitsbergen and Canadian Arctic floras. Despite the use of the North Atlantic routes by other representatives of the broad-leaved deciduous forests of the high northern latitudes, *Metasequoia* did not migrate any further to the east than eastern Greenland, the Faeroe Islands and the Isle of Mull (Seward & Edwards, 1941; Rasmussen & Koch, 1963; Boulter & Kvaček, 1989). The sub-tropical to tropical conditions that were present in Western Europe during the early Tertiary may have precluded the establishment of *Metasequoia* populations in this region at this time (Collinson, 1983). Interestingly, the genus appears to have expanded its range to eastern North America as part of the Atlantic coastal plain floras. Berry (1916) reported the occurrence of *Metasequoia* from the late Eocene Lagrange Formation of Tennessee.

In Eurasia, the populations of *Metasequoia* seen during the Late Cretaceous are no longer recorded along the shores of the Turgai Strait during the Paleocene and Eocene (Figure 1-6). This apparent absence may however be an artifact created by the lack of Paleocene and Eocene age deposits along the southeastern shores of the Turgai Strait.

The western North American and East Asian distributions of *Metasequoia* during the Oligocene differ little from that seen during the Paleocene and Eocene (Figure 1-8). Although *Metasequoia* appears to have disappeared from the polar regions, the lack of Oligocene age deposits from this part of the world might account for the apparent absence of the genus in these regions at this time. It is not known to what extent *Metasequoia* used the North Atlantic land bridges during the Paleocene and Eocene or whether the genus continued to expand further to the east in Europe at this time. Nevertheless, sea-floor spreading in the Norwegian-Greenland Sea at about the Eocene/Oligocene boundary effectively destroyed the North Atlantic land bridges and terminated all terrestrial communication between these two regions (McKenna, 1972b; Dawson *et al*., 1975, 1976; West *et al*., 1977; West & Dawson, 1978; Hoch, 1983). The significance of the North Atlantic land bridges for faunal migration between North America and Europe was recognized by McKenna (1972b) and West & Dawson (1978), who described a 30% similarity between the mammalian faunas of North America and Europe during the late Paleocene, which rose sharply to more than 50% by middle Eocene time and then dropped to about 10% following the Eocene.

Perhaps more important to the distribution pattern of *Metasequoia* were the drying of the Turgai Strait, a major global cooling event at the Eocene/Oligocene boundary and possibly, uplift of the Himalayas. The movement of polar broad-leaved deciduous forest elements, including *Metasequoia* into the West Siberian Plain is coincident with several major events (LePage, 2001, 2003a, 2003c; LePage & Basinger, 1991b, 1995). First was the drying of the Turgai Strait. The Turgai Strait was a shallow epicontinental seaway that extended from the Arctic Ocean to the Tethyan Sea, separating eastern and western Asia and effectively precluding floral and faunal exchange (McKenna, 1972b,

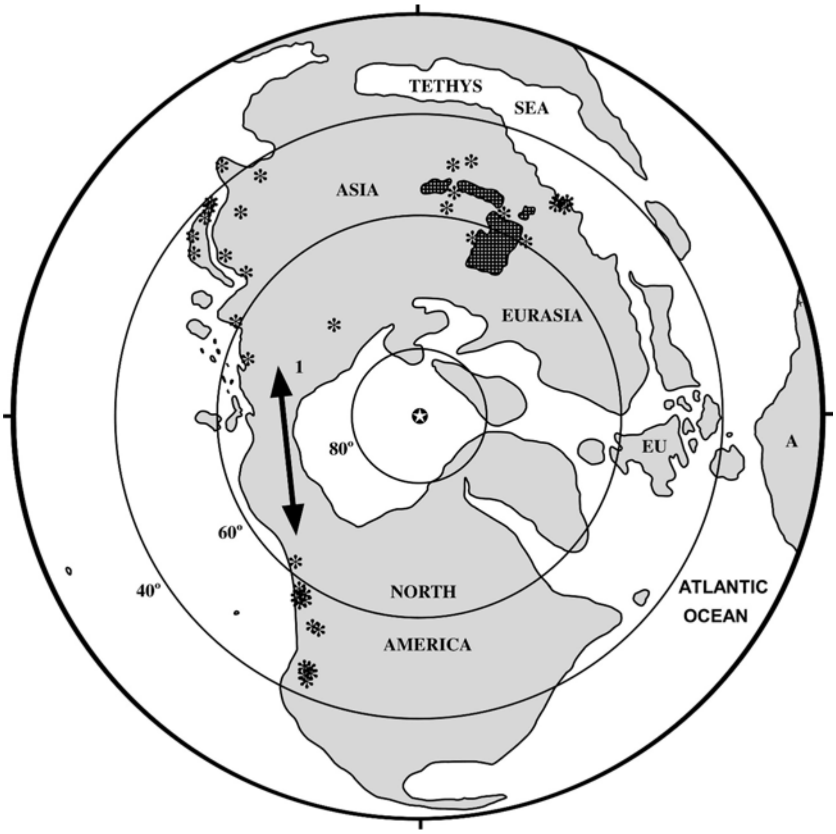

Figure 1-8. Generalized paleogeographic reconstruction of the Northern Hemisphere in polar projection during the Oligocene (ca. 29 Ma), showing the Beringian Corridor (1) and distribution of fossil *Metasequoia.* Note the spread of *Metasequoia.* from Asia into west-central Asia following regression of the Turgai Strait. The stippled region in west-central Asia indicates the location of the remnants of the Turgai Strait. *Legend:* A = Africa and EU = Europe.

1983b; Tiffney, 1985; LePage & Basinger, 1991b, 1995). McKenna (1983b) and Meng & McKenna (1998) convincingly demonstrate major faunal turnovers at the Eocene/Oligocene boundary (Bartonian/Rupelian) in western Europe and the Mongolian Plateau that are coincident with global cooling and drying of the Turgai Strait. Second, was the major global climatic cooling at the Eocene/Oligocene boundary (ca. 34 Ma) that Wolfe (1985) called the Terminal Eocene Event (TEE). Wolfe (1997) reported that 25–40% of the genera that grew in Europe, western North America and Alaska during the Eocene became extinct following the TEE. Third, the effects of the Himalayan orogeny may have created suitable habitat for *Metasequoia* along the southern margin of the

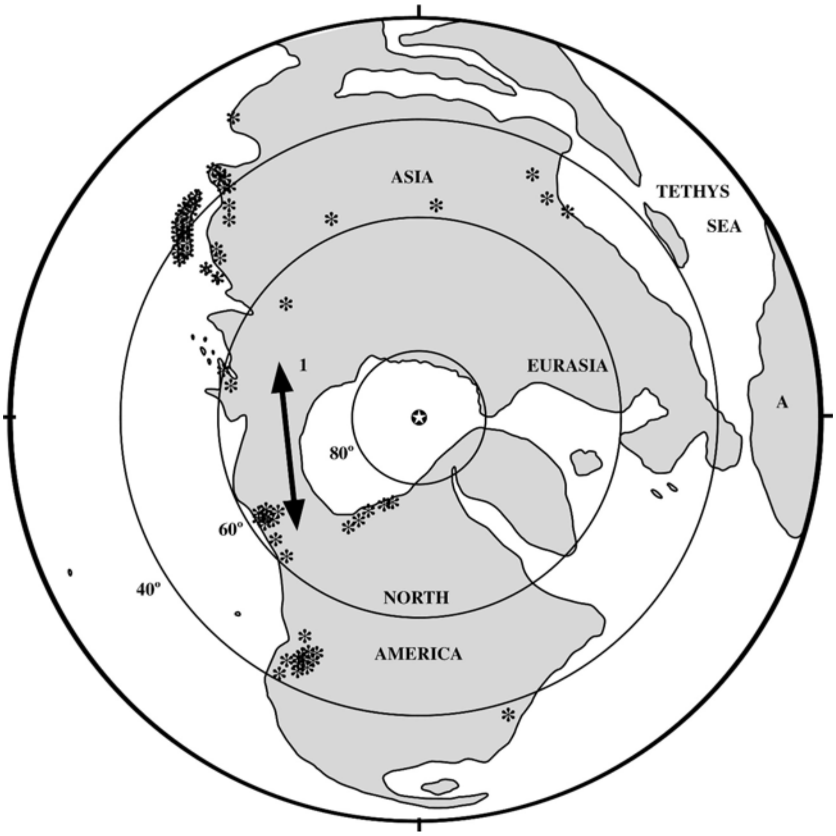

Figure 1-9. Generalized paleogeographic reconstruction of the Northern Hemisphere in polar projection during the Miocene (ca. 14 Ma), showing the Beringian Corridor (1) and the distribution of fossil *Metasequoia. Legend:* A = Africa.

Asian plate. Given that *Metasequoia* seems to thrive in regions where orogenic activity is prevalent, the southern coast of Asia may have provided suitable habitat and an extensive migratory corridor between eastern and western Asia.

By the end of the Oligocene the Turgai Strait had dried completely, climate continued to cool, and *Metasequoia* appeared in the West Siberian Plain as part of the thermophilic and mesophytic Turgai floras (Figure 1-8). However, the presence of *Metasequoia* in the West Siberian Plain appears to have been short-lived, for the genus begins to disappear from the region as climate became cooler and drier (Figure 1-9). Paleobotanical and magnetostratigraphic data from the West Siberian Plain indicate that the thermophilic and mesophytic Turgai floras of the late Oligocene and early Miocene (pre-Chron C5D) shifted to a much cooler and drier forest steppe flora by the late early-early late Miocene (Gnibidenko *et al*., 1999).

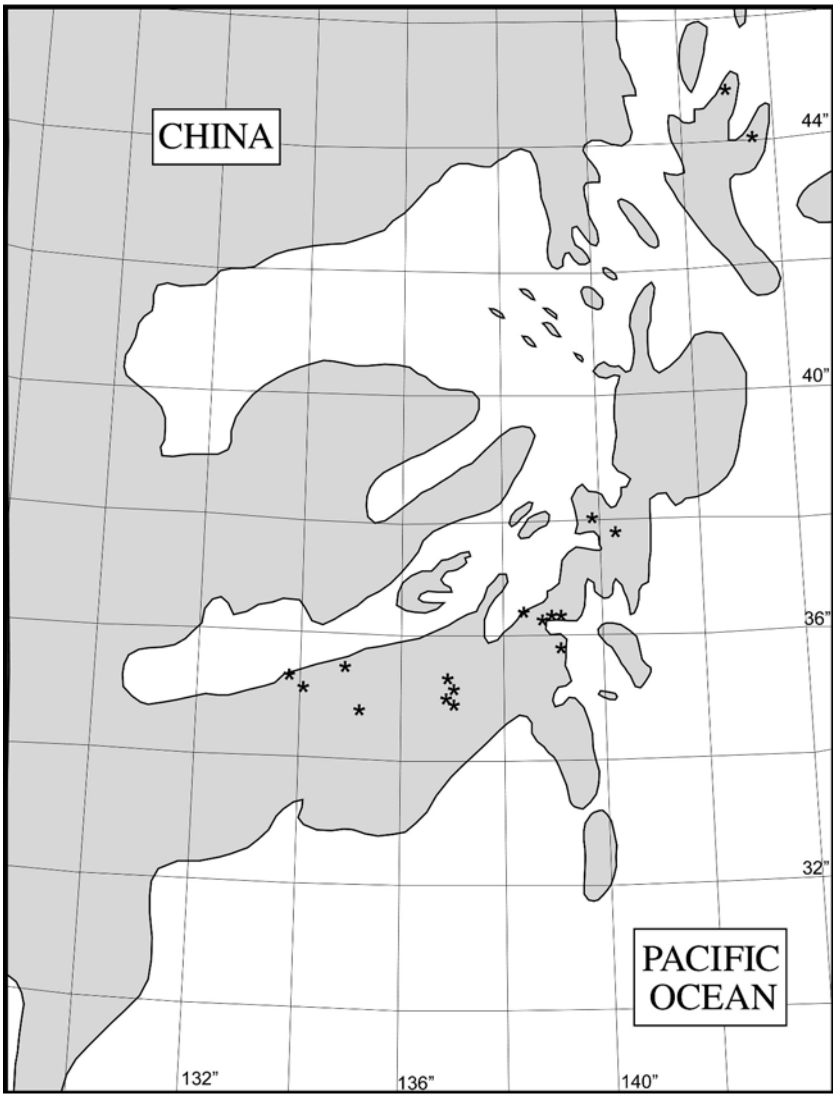

Figure 1-10. Distribution of *Metasequoia* in Japan during the late Miocene. Note the connection between southeastern Japan and the Chinese mainland. Image redrawn and modified from Minato (1965) and Yang (1991).

In North America and Asia, *Metasequoia* persisted in the mid- to high-latitude regions until Miocene time (Figure 1-9). *Metasequoia* is again recorded along the Atlantic coastal plain in the Miocene Calvert Formation of Washington, D.C. (Berry 1909). Despite the increased cooling and drying the genus persisted in the West Siberian Plain, but its distribution had shrunk considerably when compared to that seen during the Oligocene. The inability of *Metasequoia* to migrate into Europe following regression of the Turgai Strait together with other thermophilic and mesophytic elements of the broad-leaved deciduous forests such as *Larix* Miller, *Tsuga* (Endlicher) Carrière, *Picea* A. Dietrich and *Taiwania* Hayata (LePage & Basinger, 1991a; LePage, 2001, 2003a, 2003c, unpublished) remains unexplained.

The late Miocene distribution of *Metasequoia* in Japan indicates that the genus was well represented in Hokkaido and Honshu (Figure 1-10). It is important to note that Japan was connected to the Chinese mainland at this time providing a floral conduit between these two areas. By Pliocene time, habitat partitioning as well as climate and environmental changes caused *Metasequoia* to disappear from Hokkaido (Momohara, 1997, this volume). The populations in Honshu persisted and the genus became established in Shikoku and Kyushu (Figure 1-11). Moreover, the land connection that existed between Japan and the Chinese mainland during the late Miocene was severed during the Pliocene. During the late Pliocene and early Pleistocene *Metasequoia* was well represented in central and southern Japan and the land bridge between Japan and the Chinese mainland was again re-established (Figure 1-12).

With few exceptions the plant fossil record indicates that *Metasequoia* disappeared from the rest of the world during the late Miocene and Pliocene. Late Pliocene occurrences of *Metasequoia* include reports from Arctic Canada (Matthews & Ovenden, 1990; Matthews *et al.*, 1990) and western Siberia (Gorbunov, 1957, 1962) and Chochieva (1975) indicates that *Metasequoia* persisted until the late Pliocene-early Pleistocene in western Georgia. *Metasequoia* became extinct in Japan during the latest early Pleistocene, about 1.1 to 0.8 million years ago (Momohara, 1994, this volume; Momohara *et al.*, 1990). Given that *Metasequoia* can tolerate temperatures ranging from 40°C to –40°C (Sakai & Larcher, 1987; LePage, unpublished), its demise might have been associated with increasing global aridity, rather than cooler temperatures (Momohara, this volume).

As pointed out by Yang & Jin (2000), the extirpation of *Metasequoia* from China and its re-appearance in present day Sichuan, Hubei and Hunan Provinces is an enigma that elicits at least two major questions. First, did *Metasequoia* survive in southeast China throughout the Pliocene and Pleistocene without being preserved or detected in the plant fossil record? Fossil wood identified as *M. glyptostroboides* was excavated from Wuhan City and dated as being 11,280 ± 190 years B.P. (Qi *et al.*, 1993). If this report were accurate, it would then indicate that the genus was much more widespread in China during the recent past and that *Metasequoia* was present in China during Pleistocene time. Alternatively, did *Metasequoia* become extinct in China at the close of the Miocene only to become re-established from the Japanese populations sometime before the latest early Pleistocene? Minato (1965) and Yang

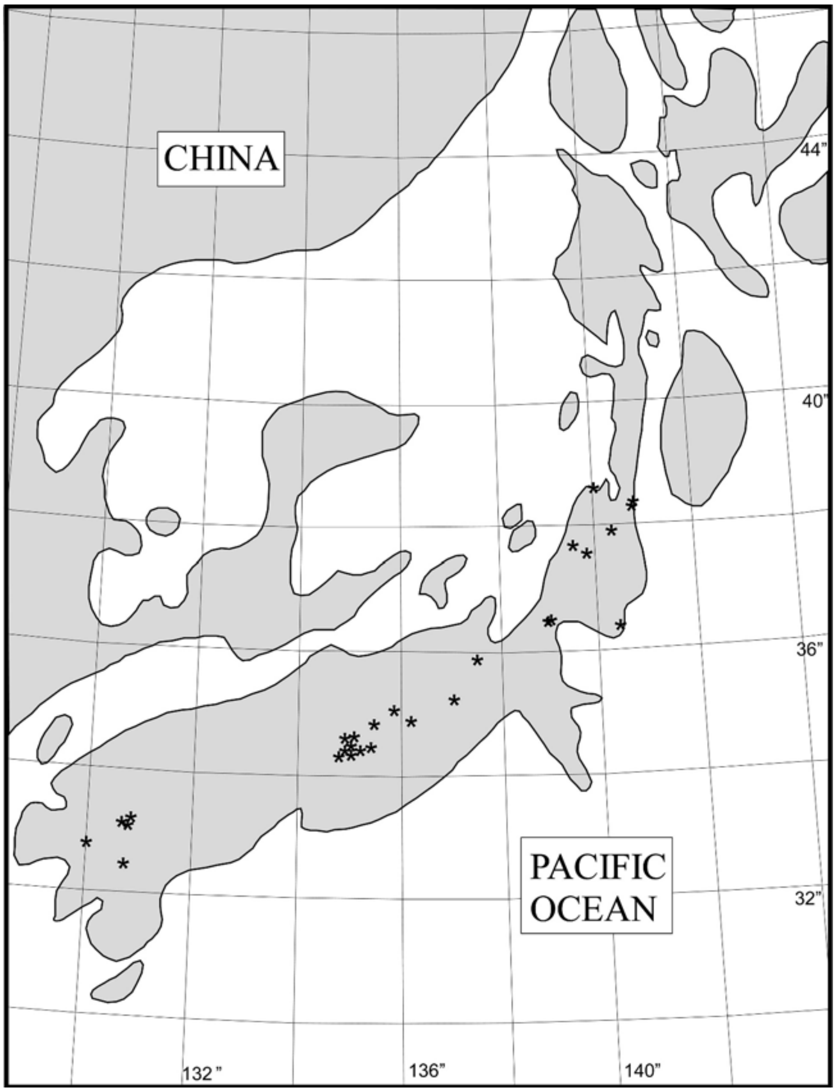

Figure 1-11. Distribution of *Metasequoia* in Japan during the Pliocene. Note that the connection between southeastern Japan and the Chinese mainland that was present during the late Miocene is now broken. Image redrawn and modified from Minato (1965) and Yang (1991).

(1991) indicate that Japan temporarily re-established land connections with China a number of times during Plio-Pleistocene time. Clearly the answer to these questions will require detailed paleobotanical and archaeological studies that are focused on late Tertiary and Quaternary deposits so that the vegetation history of southeast China can be reconstructed in detail.

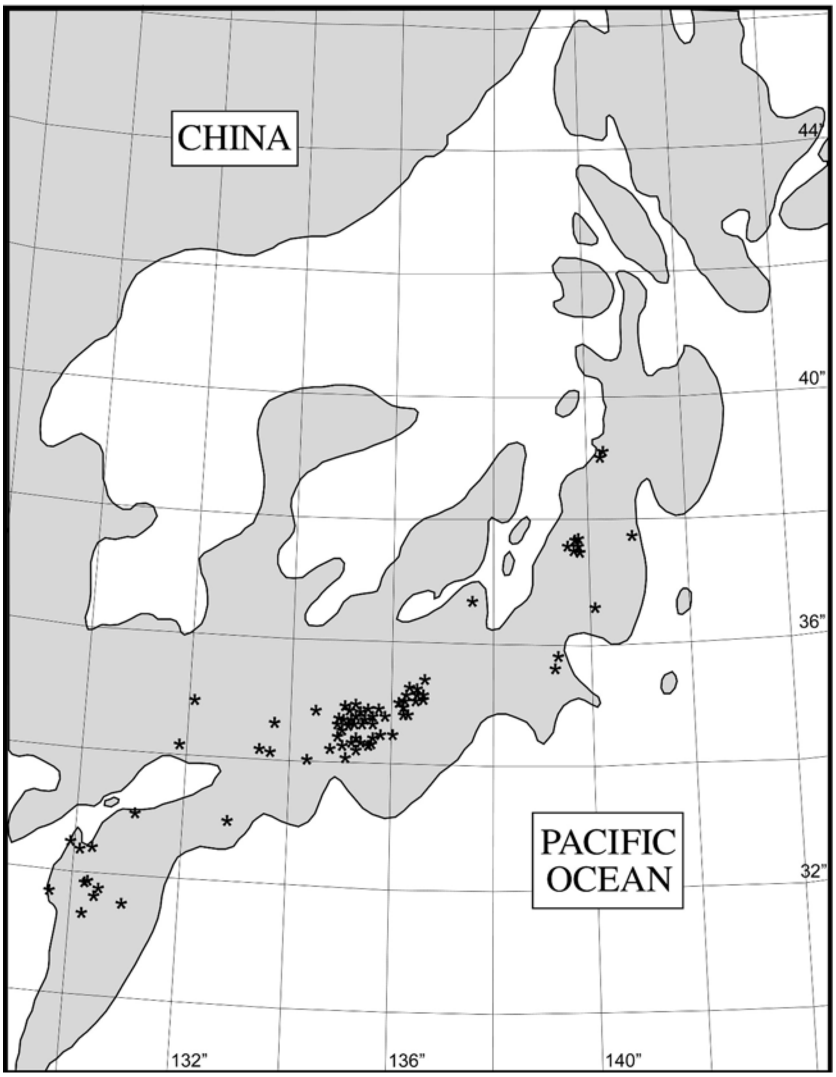

Figure 1-12. The distribution of *Metasequoia* in Japan during the Plio-Pleistocene. Note that the connection between southeastern Japan and the Chinese mainland has been re-established. Image redrawn and modified from Minato (1965) and Yang (1991).

6. PUTATIVE *METASEQUOIA* REMAINS FROM EUROPE

Although there have been a number of reports of fossil *Metasequoia* wood, leaves, seeds and cones from Europe (e.g., Schönfeld, 1955; Zalewska, 1959), the validity of these reports has been questioned (Dorofeev & Sveshnikova, 1963). Throughout the Tertiary the plant fossil record indicates that *Metasequoia* and *Glyptostrobus* co-existed in some lowland swamp forest communities (e.g., Basinger, 1991; Richter & LePage, this volume). However, in the absence of diagnostic leaves and seed cones, the fossil *Metasequoia* wood has been difficult to separate from that of *Glyptostrobus*. Recently, Visscher & Jagels (2003) have shown that it is possible to discriminate between the wood of living representatives of these two genera if a sufficient sample size is available. To determine whether Schönfeld's identification is valid, we recommend that the putative fossil *Metasequoia* wood described by Schönfeld (1955) from the German Miocene browncoals of Düren be re-examined or that additional material be re-collected from the locality where it was first found.

The descriptions and illustrated material of *Metasequoia europaea* Zalewska provided by Zalewska (1959) are interesting and the unilateral conclusion that *Metasequoia* did not occupy Europe should not be dismissed without further study. Given that the genus had reached western Asia/eastern Europe by the Late Cretaceous (Maastrichtian; Figure 1-5), eastern Greenland and western Europe (Isle of Mull and Faeroe Islands; Figure 1-6) during the early Tertiary and persisted in southern Caucasus until the Plio-Pleistocene (Chochieva, 1975), there is no reason why *Metasequoia* should not have been a part of the warm-temperate broad-leaved deciduous forests that began to emerge in this part of the world during the mid- to late Tertiary. The fact that floral elements such as *Tsuga* and *Taiwania*, genera that co-existed with *Metasequoia* in the Canadian Arctic and constituents of the warm-temperate broad-leaved deciduous forests (LePage, 2003a; Richter & LePage, this volume), were reported in Europe during the early Tertiary indicates that the climatic and environmental conditions were suitable for *Metasequoia* to thrive (LePage, 2003a, unpublished). A re-investigation of the *Sequoia* and *Taxodium* fossils, as well as the other taxa that fossil *Metasequoia* has been assigned to in the past (Appendix A) may provide the answer to this enigma.

7. OROGENIES AND ECOLOGICAL COMPETITION

The fossil record of *Metasequoia* indicates that the genus first appeared as a minor constituent of the Late Cretaceous floras of Russia and North America, then became a dominant constituent of the early Tertiary floras of Asia and North America before its final extinction in North America and Asia during the late Tertiary. Although explanations for the demise of the genus have focused on global cooling and increased aridity (Yang & Jin, 2000; Momohara, 1997, this volume), the distribution of *M. glyptostroboides* trees planted in arboreta throughout the world indicate that *M. glyptostroboides* is capable of growing under a wide rage of temperatures, though it is much more sensitive to aridity (Xie *et al*., 1999a, 1999b; Williams, this volume).

Despite the ability of *M. glyptostroboides* to grow under a wide range of climatic and environmental conditions, its extensive range during the early Tertiary shrunk considerably and the number of trees growing in its native habitat today number about 5,000 individuals. Clearly, global cooling and increasing aridity alone do not provide a satisfactory explanation for the near extinction of the genus. However, at the time the genus began to experience range reduction several prominent changes were occurring. If we consider factors such as: physical mechanisms of global climate; changes in the regional landscapes; the emergence of new vegetation formations; and increased competition for space and resources, a possible explanation for *Metasequoia's* decline begins to emerge. To do this we have compared the relative abundance of representatives of the Taxodiaceae to that of the Pinaceae.

Throughout the Late Cretaceous and early Tertiary the representatives of the Taxodiaceae were much more abundant and geographically widespread than those of the Pinaceae (Florin, 1963) despite the initiation of major global tectonic events such as sea-floor spreading in the north Atlantic and uplift of the Himalayas and Rocky Mountains. It is during the Miocene that changes in the relative abundance between these the Taxodiaceae and Pinaceae become apparent. During the Miocene two trends are recognised. First the geographic range and abundance of representatives of the Taxodiaceae such as *Metasequoia* decrease (Jongmans & Dijkstra, 1971–1974; Dijkstra & Schaarschmidt, 1975). Second, the geographic ranges and number of Pinaceae species described from the plant fossil record throughout North America and Asia increase (Jongmans & Dijkstra, 1971–1974; Dijkstra & Schaarschmidt, 1975). These trends appear to be related to large-scale habitat creation and partitioning associated with mountain-building events and subsequent global cooling (Figure 1-13).

In North America, thermal uplift of the Western Cordillera began during the middle Miocene and the elevation of the region rose from about 1,000 m to 4,000–4,500 m (Omar *et al.*, 1994). Ecologically, an event of this magnitude was significant, for it created an altitudinally continuous environmental gradient from the low-elevation warm temperate zone to the high-elevation cool temperate and boreal/montane floristic zones. Using the world-wide mean lapse rate of 5.5°C/1,000 m (Wolfe, 1992), the temperature at 4,000 to 4,500 m would have been about 16.5 to 19°C cooler than that seen at 1,000 m, which was probably cold enough to establish a tree line and alpine habitats. On the eastern side of the Western Cordillera, the effects of the rising mountains would have created a rain shadow resulting in an overall decrease in local and regional rainfall and increased aridity.

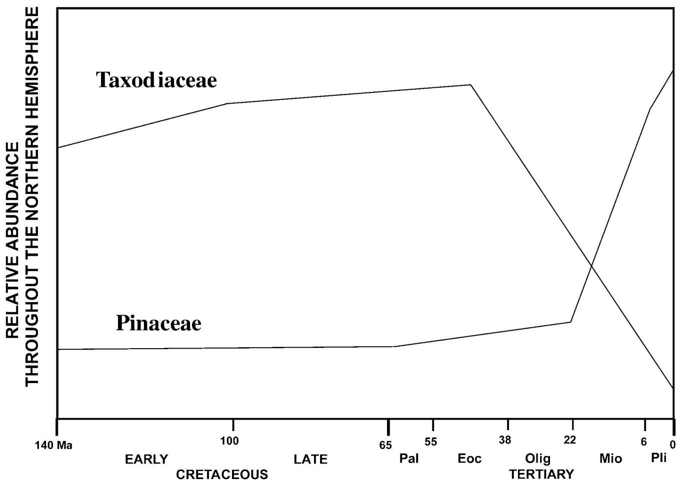

Figure 1-13. Relative abundance of Taxodiaceae as compared to members of the Pinaceae. Note that the relative abundances remain more or less unchanged until Miocene time.

In Asia, uplift of the Himalayas and Tibetan Plateau occurred at about mid-Miocene time, with significant uplift occurring during the late Miocene (Yoshida, 1984; Johnson *et al.*, 1982; Burbank & Johnson, 1983; Mercier *et al.*, 1987; Ruddiman & Kutzbach 1989; Ruddiman *et al.*, 1989). During the late Miocene (5–10 Ma) estimates of 2,500 to 4,000 m of uplift have been proposed, while palynofloral and faunal remains indicate that uplift of the Tibetan Plateau was at least 2,000 m (Hsü, 1978; Liu & Ding, 1984; Mercier *et al.*, 1987). To the north and northeast of the Himalayas, decreased rainfall and increased aridity would have resulted.

These two events together with the global cooling trend were advantageous for plants that were able to tolerate colder temperatures and other environmental stresses not encountered at the lower elevations. However as previously pointed out, *Metasequoia* can tolerate cold to freezing conditions and the creation of new, unstable environments such as those seen in montane environments would have favoured the establishment of extensive *Metasequoia* forests. Clearly other factors precluded the establishment of *Metasequoia* from these emerging habitats. If we consider the nutrient-acquisition strategies and the fungal symbionts utilised by the Pinaceae and Taxodiaceae, a possible explanation begins to emerge.

Read (1984) has proposed that the mycorrhizal strategy employed by plants broadly corresponds to the environment in which they occur (Figure 1-14). The Pinaceae support ectomycorrhizal symbionts, while representatives of the Taxodiaceae support endomycorrizal associations. Thus, in most forests

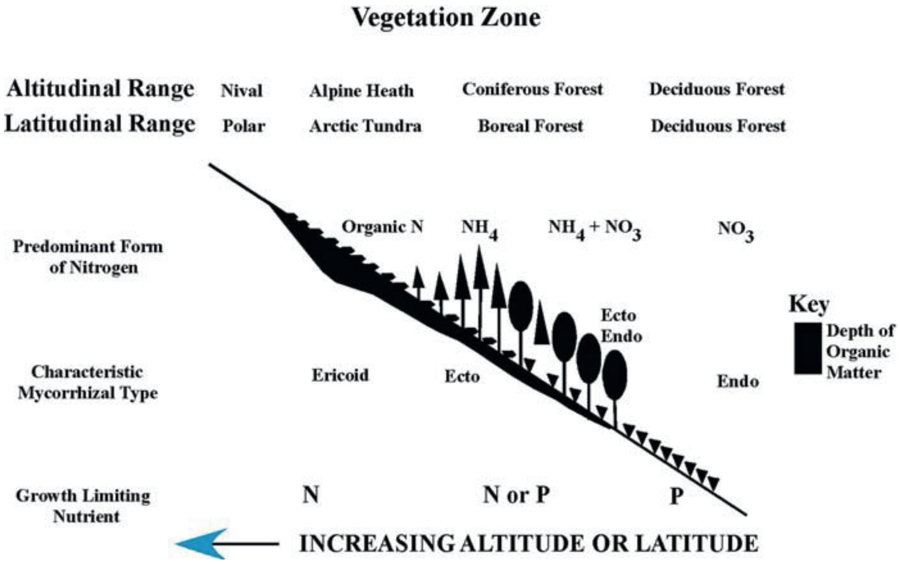

Figure 1-14. Simplified diagram depicting the putative relationship between altitude, latitude, climate, forest type and mycorrhizal type. Redrawn and modified from Read (1984).

growing on mineral- and nutrient-rich soils at low latitudes and altitudes where the temperature is warm and organic turnover is high, plants utilising an endomycorrhizal strategy tend to dominate the landscape. As altitude and latitude increase, the temperature becomes cooler and sometimes drier (depending on aspect) and the rate of biomass accumulation becomes greater than decomposition. In these boreal and cool temperate environments, plants forming ectomycorrhizal associations such as the Pinaceae dominate the landscape. The soils in these environments tend to be organic-rich and depending on the soil conditions, the nitrogen and phosphorous pools are commonly comprised of organic forms that are generally not available to plants (Smith & Read, 1997). Thus, the ectomycorrhizal fungi associated with plants growing in acid organic soils where the nitrogen and phosphorous pools consist of organic forms, produce extracellular enzymes that are capable of degrading the organic components of the forest-floor litter to absorb and mobilise the nitrogen and phosphorus needed by the plants (Smith & Read, 1997).

Therefore, the newly emerging late Miocene and Pliocene high-altitude montane environments of western North America and Asia, together with the global cooling trend that began near the end of the Eocene, increased aridity and nutrient-acquisition strategies would have favored the spread and evolution of ectomycorrhizal plants, such as the Pinaceae.

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10. APPENDIX A

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***Taxites olriki* Heer *var. brevioribus obtusis* Heer**: Heer, *Flora Fossilis Arctica* 7: 56 (1883a).

***Taxites pectens* Heer**: Heer, *Flora Fossilis Arctica* 7: 9, pl. 53, figs. 9, 9b (1883a).

***Taxites validus* Heer**: Heer, *Kungliga Svenska Vetenskaps-Akademiens Handlingar* 13: 13, pl. 1, fig. 11 (1874).

Taxites validus Heer: Heer, *Flora Fossilis Arctica* 7: 56 (1883a).

***Taxites* sp., Nathorst**, *Kungliga Svenska Vetenskaps-Akademiens Handlingar* 20: 35, pl. 1, fig. 8 (1883).

***Taxodium crassum* Hollick**: Hollick, *United States Geological Survey, Professional Paper* 182: 48, pl. 64, fig. 4b only (1936).

***Taxodium cuneatum* Newberry**: Newberry, *Boston Journal of Natural History* 7: 517 (1863).

Taxodium cuneatum Newberry: Dawson, *Proceedings and Transactions of the Royal Society of Canada* 1: 25 (1882).

Taxodium cuneatum Newberry: Knowlton, *United States Geological Survey, Bulletin* 152: 226 (1898a).

***Taxodium distichum* Richard**: Penhallow, *Proceedings and Transactions of the Royal Society of Canada, 2nd Series* 9: 36, fig.1 (1903).

Taxodium distichum Richard: Penhallow, *Proceedings and Transactions of the Royal Society of Canada 3rd Series* 1: 301 (1907a).

Taxodium distichum Richard: Penhallow, *A Manual of the North American Gymnosperms*, p. 217–218 (1907b).

Taxodium distichum Richard: Penhallow, *Proceedings and Transactions of the Royal Society of Canada, 2nd Series* 8: 301 (1908).

***Taxodium distichum angustifolium* Heer**: Heer, *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg* 25: 52, pl. 15, figs. 10–12 (1878b).

***Taxodium distichum miocenum* Heer**: Heer, *Flora Fossilis Arctica* 2: 21, pl. 1, fig. 6; pl. 3, fig. 11c; pl. 4, figs. 5b–5c (1869).

Taxodium distichum miocenum Heer: Heer, *Flora Fossilis Arctica* 2: 32, pl. 3, figs. 30–31; pl. 16, figs. 8b–8c (1870a).

Taxodium distichum miocenum Heer: Heer, *Philosophical Transactions of the Royal Society* 159: 463, pl. 43, figs. 4–5 (1870b).

Taxodium distichum miocenum Heer: Heer, *Kungliga Svenska Vetenskaps-Akademiens Handlingar* 13: 9, 13, 19, pl. 1, figs. 4b, 13c–13d, 15b; pl. 2, figs. 20d, 21; pl. 4, fig. 5 (1874).

Taxodium distichum miocenum Heer: Heer, *Flora Fossilis Arctica* 4: 57, pl. 13, figs. 12–13; pl. 25, figs. 9b, 13 (1876).

Taxodium distichum miocenum Heer: Heer, *Flora Fossilis Arctica* 5: 23, pl. 2, figs. 1b–9 (1878a).

Taxodium distichum miocenum Heer: Heer, *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg* 25: 33, 48, pl. 8, fig. 25b; pl. 9, fig. 1; pl. 15, figs. 1–2 (1878b).

Taxodium distichum miocenum Heer: Heer, *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg* 25: 22, pl. 1, fig. 9 (1878c).

Taxodium distichum miocenum Heer: Heer, *Kungliga Svenska Vetenskaps-Akademiens Handlingar* 15: 4 (1878d).

Taxodium distichum miocenum Heer: Lesquereux, *10th Annual Report of the United States Geological and Geographical Survey*, p. 498 (1878a).

Taxodium distichum miocenum Heer: Heer, *Kungliga Svenska Vetenskaps-Akademiens Handlingar* 18: 9 (1880a).

Taxodium distichum miocenum Heer: Heer, *Flora Fossilis Arctica* 6: 12 (1880b).

Taxodium distichum miocenum Heer: Heer, *Flora Fossilis Arctica* 7: 60, pl. 70, fig. 11; pl. 87, fig. 7; pl. 88, fig. 2b; pl. 96, figs. 8–9 (1883a).

Taxodium distichum miocenum Heer: Yokoyama , *Bulletin of the Geological Society of Japan, Part A*, 1: 221, 223 (1886).

Taxodium distichum miocenum Heer: Nathorst, *Palaeontologische Abhandlungen* 4: 7, pl. 1, fig. 4 (1888).

Taxodium distichum miocenum Heer: Dawson, *Royal Society of Canada, Transactions* 8: 79, text-fig. 6 (1891).

Taxodium distichum miocenum Heer: Knowlton, *Geological Society of America, Bulletin* 5: 578 (1893a).

Taxodium distichum miocenum Heer: Knowlton, *United States Geological Survey, Bulletin* 105: 46 (1893b).

Taxodium distichum miocenum Heer: Knowlton, *Proceedings of the United States National Museum* 17: 214 (1894).

Taxodium distichum miocenum Heer: Knowlton, *United States Geological Survey, Annual Report* 17: 878 (1896).

Taxodium distichum miocenum Heer: Newberry, *United States Geological Survey Monograph* 35: 22, pl. 47, fig. 6; pl. 51, fig. 3; pl. 52, figs. 2–4; pl. 55, fig.5 (1898).

Taxodium distichum miocenum Heer: Knowlton, *United States Geological Survey, Bulletin* 152: 226 (1898a).

Taxodium distichum miocenum Heer: Knowlton, *United States Geological Survey, Bulletin* 204: 27 (1902).

Taxodium distichum miocenum Heer: Penhallow, *Proceedings and Transactions of the Royal Society of Canada, 2nd Series* 8: 51, 68 (1902).

Taxodium distichum miocenum Heer: Knowlton, *Harriman Alaska Expedition* 4: 152 (1904).

Taxodium distichum miocenum Heer: Penhallow, *Geological Survey of Canada, Annual Report for 1904, New Series* 16: 389A, 391A (1906).

Taxodium distichum miocenum Heer: Penhallow, *Report on Tertiary Plants of British Columbia*, p. 91 (1908).

Taxodium distichum miocenum Heer: Berry, *Journal of Geology* 17: 22, fig. 1 (1909).

Taxodium distichum miocenum Heer: Knowlton, *Proceedings of the Washington Academy of Sciences* 11: 204, 207, 215 (1909).

Taxodium distichum miocenum Heer: Smith & Duror, *Journal of Geology* 24: 573, figs. 5c, 7d (1916).

Taxodium distichum miocenum Heer: Kryshtofovich, *Journal of the Geological Society, Tokyo* 27: 10, 14, 17 (1920).

Taxodium distichum miocenum Heer: Kryshtofovich, *Materials on the Geology and Fossil Plants of the Far East* 18: 2 (1921a).

Taxodium distichum miocenum Heer: Ichimura, *Korean Coal-Field Research Report* 1: 9 (1927).

Taxodium distichum miocenum Heer: Kryshtofovich, *Annals of the Russian Paleontological Society* 8: 14, 25 (1930).

Taxodium distichum miocenum Heer: Endo, *Iwanami Geology and Paleontology Series* 24: 6, 8, 16 text-fig. 1 (1931).

Taxodium distichum miocenum Heer: Kon'no, *Geology of Central Shinano*, pl. 8, figs. 1–2 (1931).

Taxodium distichum miocenum Heer: Morita, *Japanese Journal of Geology and Geography* 9: 3 (1932).

Taxodium distichum miocenum Heer: Endo, *Journal of the Geological Society of Japan* 45: 88 (1938a).

Taxodium distichum miocenum Heer: Shikama, *Journal of the Geological Society of Japan* 45: 628 (1938).

***?Taxodium distichum* Richard**: Florin, *Kungliga Svenska Vetenskaps Akademiens Handlingar* 61: 16, 30, pl. 1 figs. 1–2; pl. 5, figs. 10–11 (1920).

***Taxodium distichum dubium* Cockerell**: Cockerell, *American Naturalist* 44: 35 (1910).

***Taxodium distichum* Rich. *var. miocaenum* Heer**: Kryshtofovich, *Botanical Journal* 31: 17, text-fig. 1 (1946).

***Taxodium distichum miocenum var. angustifolium* Heer**: Lesquereux, *Proceedings of the United States National Museum* 11: 34 (1889).

***Taxodium dubium* (Sternberg) Heer**: Heer, *Flora Fossilis Arctica* 1: 89, 156, pl. 2, figs. 24–27; pl. 12, fig. 1c; pl. 30, figs. 3–4; pl. 45, figs. 11d, 12d (1868).

Taxodium dubium (Sternberg) Heer: Lesquereux, *6th Annual Report of United States Geological Survey of the Territories*, p. 389 (1873).

Taxodium dubium (Sternberg) Heer: Lesquereux, *7th Annual Report of United States Geological Survey of the Territories*, p. 388, 409 (1874).

Taxodium dubium (Sternberg) Heer: Lesquereux, *10th Annual Report of the United States Geological and Geographical Survey*, p. 498 (1878a).

Taxodium dubium (Sternberg) Heer: Berry, *United States Geological Survey, Professional Paper* 91: 171–173, pl. 15, figs. 4–6 (1916).

Taxodium dubium (Sternberg) Heer: Berry, *Geological Survey of Canada, Bulletin* 42: 97 (1926a).

Taxodium dubium (Sternberg) Heer: Berry, *Transactions of the Royal Society of Canada, 3rd Series* 20: 191 (1926b).

Taxodium dubium (Sternberg) Heer: Knowlton, *United States Geological Survey, Professional Paper* 140: 27–28, pl. 9, figs. 2, 7–9; pl. 10, fig. 2 (1926).

Taxodium dubium (Sternberg) Heer: Berry, *National Museum of Canada, Memoir* 63: 18 (1930).

Taxodium dubium (Sternberg) Heer: Williams & Dyer, *Geological Survey of Canada, Memoir* 163: 64 (1930).

Taxodium dubium (Sternberg) Heer: Berry, *Geological Survey of Canada, Memoir* 182: 19 (1935).

Taxodium dubium (Sternberg) Heer: Hollick, *United States Geological Survey, Professional Paper* 182: 48, pl. 16, fig. 5; pl. 51, fig. 5a (1936).

Taxodium dubium (Sternberg) Heer: MacGinitie, *Carnegie Institute of Washington, Publication* 465: 132, pl. 3, fig. 4 (1937).

Taxodium dubium (Sternberg) Heer: Gabrielse, *Geological Survey of Canada, Memoir* 319: 95 (1963).

Taxodium dubium (Sternberg) Heer: Makulbekov, *Academia Nauk Kazakhstan SSR, Zoology Institute* 6: 110, pl. 1, figs. 2–3 (1974).

Taxodium gracile **Heer**: Heer, *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg* 25: 33, pl. 8, figs. 30b, 31–37 (1878b).

Taxodium occidentale **Newberry**: Newberry, *Boston Journal of Natural History* 7:516 (1863).

Taxodium occidentale Newberry: Newberry, *Annals of the Lyceum of Natural History* 9: 45 (1868).

Taxodium occidentale Newberry: Dawson, *Canada Geological Survey, Report of Progress for 1875–76*, p. 260 (1877).

Taxodium occidentale Newberry: Lesquereux, *10th Annual Report of the United States Geological and Geographical Survey*, p. 498 (1878a).

Taxodium occidentale Newberry: Lesquereux, *Illustrations of Cretaceous and Tertiary Plants*, pl. 11, figs. 1–3 (1878b).

Taxodium occidentale Newberry: Newberry, *United States Geological Survey Monograph* 35: 23, pl. 26, figs. 1–3; pl. 55, fig. 5 (1898).

Taxodium occidentale Newberry: Knowlton, *United States Geological Survey, Bulletin* 152: 226 (1898a).

Taxodium occidentale Newberry: Penhallow, *Geological Survey of Canada, Annual Report for 1904*, New Series 16: 390–391A (1906).

Taxodium occidentale Newberry: Penhallow, *Report on Tertiary Plants of British Columbia*, p. 91 (1908).

Taxodium occidentale Newberry: Knowlton, *Proceedings of the Washington Academy of Sciences* 11: 185, 189, 195–196, 202–203, 211, 214–215 (1909).

Taxodium occidentale Newberry: Knowlton, *Journal of Geology* 19: 369 (1911).

Taxodium occidentale Newberry: Martin & Katz, *United States Geological Survey, Bulletin* 500, p. 51 (1912).

Taxodium occidentale Newberry: Berry, *Geological Survey of Canada, Bulletin* 42: 97, pl. 10, fig. 1 (1926a).

Taxodium occidentale Newberry: Berry, *Transactions of the Royal Society of Canada, 3rd Series* 20: 190 (1926b).

Taxodium occidentale Newberry: Berry, *Geological Survey of Canada, Memoir* 182: 19–20 (1935).

Taxodium occidentale Newberry: Hollick, *United States Geological Survey, Professional Paper* 182: 50, pl. 16, fig. 3; pl. 109, figs. 9–10 (1936).

Taxodium occidentale Newberry:Wickenden, *Geological Survey of Canada, Memoir* 239: 51 (1963).

Taxodium tinajorum **Heer**: Heer, *Flora Fossilis Arctica* 2: 22, pl. 1, figs. 1–5 (1869).

Taxodium tinajorum Heer: Heer, *Flora Fossilis Arctica* 4: 57, pl. 25, fig. 14 (1876).

Taxodium tinajorum Heer: Heer, *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg* 25: 33, pl. 8, figs. 30a, 38 (1878b).

Taxodium tinajorum Heer: Lesquereux, *10^{th} Annual Report of the United States Geological and Geographical Survey*, p. 498 (1878a).

Taxodium tinajorum Heer: Lesquereux, *Proceedings of the United States National Museum* 11: 34 (1889).

Taxodium tinajorum Heer: Knowlton, *Geological Society of America, Bulletin* 5: 578 (1893a).

Taxodium tinajorum Heer: Knowlton, *Proceedings of the United States National Museum* 17: 214 (1894).

Taxodium tinajorum Heer: Knowlton, *United States Geological Survey, Annual Report* 17: 878 (1896).

Taxodium tinajorum Heer: Knowlton, *United States Geological Survey, Bulletin* 152: 226 (1898a).

Taxodium tinajorum Heer: Knowlton, *Harriman Alaska Expedition* 4: 152 (1904).

Taxodium tinajorum Heer: Hollick, *United States Geological Survey, Professional Paper* 182: 50–51, pl. 10, fig. 4; pl. 13, figs. 2–3, 5–6; pl. 18, fig. 5b (1936).

***Taxodium* sp., Dawson**, *Proceedings and Transactions of the Royal Society of Canada* 11: 56, pl. 6, fig. 10 (1893).

***Taxodium* sp., Dawson**: Knowlton, *United States Geological Survey, Bulletin* 152: 226 (1898a).

***Taxodium*? sp., Endo**, *Journal of Geography, Tokyo* 38: 636 (1926).

***Taxodium* sp., Ichimura**, *Korean Coal-Field Research Report* 1: 10 (1927).

***Taxodium* sp. *indet*., Schloemer-Jäger**, *Palaeontographica, Abteilung B, Pälaophytologie* 104: 61–62, pl. 9, fig. 3; text-figs. 12 (1958).

***Taxodium* (?), Gardner**, *A Monograph of British Eocene Floras*, pl. 27, fig. 3 (1886).

***Taxodium* sp. (*T. cfr. tinajorum* Heer) Endo**, *Journal of the Geological Society of Japan* 45: 89 (1938a).

***Taxus* sp. Mason**, *Carnegie Institute of Washington, Publication* 346: 146, pl. 1, fig. 4 (1927).

***Taxus* sp. Chaney**, *Carnegie Institute of Washington, Publication* 346: 102 (1927).

Torreya densifolia Dawson, *Proceedings and Transactions of the Royal Society of Canada* 1: 25, pl. 5, figs 20, 20a (1882).

***Tumion densifolium* (Dawson) Knowlton**: Knowlton, *United States Geological Survey, Bulletin* 152: 234 (1898a).

***Tumion*? *suspectum* Hollick (*nomen nudum*)**: Hollick, *United States Geological Survey, Professional Paper* 159: 55, pl. 19, figs. 4–6a; pl. 29, fig. 1b (1930).

11. APPENDIX B

Included here are references to sources of published data on the fossil record of *Metasequoia* that extend from Late Cretaceous to Pleistocene time. Although the authors have sought to provide a list as complete as possible, we are aware that there are gaps. Because of the problems associated with reliably identifying fossil *Metasequoia* wood and pollen, references dealing with these types of remains were omitted. No attempts were made to determine the accuracy of the taxonomic and nomenclatural information of all of the fossil species. However, the authors would like to point out that the number of *Metasequoia* specimens residing in collections that have not yet been identified or described is likely to be considerable. Inclusion of these specimens would be of considerable benefit, but this exercise is far outside of the scope of this paper. With few exceptions (i.e., those that the authors have visited personally) or unless indicated in the literature, most of the latitudes and longitudes should be considered approximate and represent the current position of the deposits, rather than their paleo-positions. Unknown geologic formations are listed as "undefined".

11.1. Russia and Former Countries of the USSR

1. Arkagala Coal Basin, upper Kolyma River (ca. 68°N, 153–154°E), Arkagala Formation, Cenomanian (Samylina, 1962; Lebedev, 1976).
2. Arkagala River (63°08'N, 147°01'E), Arkagala and Dolgin Formations, Cenomanian (Samylina, 1988).
3. Okhotsk-Chukotka Volcanigenic Belt, Ul'inskiy Trough near Amka (59°02'N, 140°42'E), Amkinian flora (Uyenminian, Ust'Amkinian and Gyrbykanian assemblages), Amkinskaya Formation, Cenomanian (Baikovskaya, 1956; Lebedev, 1979, 1982, 1987).
4. Vilyuya, Linde, Tyung, Chibida and Tangnaryi Rivers, near Vilyuysk (63°40'N, 121°00'E), Lower Agraphenian floristic complex, Late Cenomanian/Turonian and Lower Chirimyian-Upper Chirimyian, Early to Late Senonian (Sveshnikova, 1967).
5. New Siberia Island (74°50'N, 139°40'E), undefined, Turonian (Baikovskaya, 1956).
6. Zhubankari Mountain near Lake Zaisan (48°05'N, 84°10'E), undefined, Senonian (Shilin & Romanova, 1978).
7. Ulen-Kalkan (ca. 43°51'N, 77°14'E), Iliysk Depression, Ili River Basin, undefined, Maastrichtian (Makulbekov, 1974).
8. Amaan Lagoon, Ilnaivaam and Emima Rivers (62°35'N 179°26'E), Kamchatka Peninsula, Koryak Formation, Late Maastrichtian (Budantsev,

1983; Golovneva & Herman, 1992, 1998; Golovneva 1994a, 1994b; Herman, 1993; Herman & Spicer, 1995, 1997).

9. Eloguy (Yeloguy) River (62°55'N 87°18'E), Krasnoyarsk Province, lower part of the Pokurskoi Formation, Late Cretaceous (Lebedev, 1962).
10. Near Bogopoli (44°16'N, 135°25'E), Sikhote Alin, Taxobinskoi and Bogopoliskoi Formations, Maastrichtian-early Paleocene (Ablaev, 1974).
11. Anadyr, Lamutskaya, Gornaya, Umku-veem and Euchuvytkin Rivers (64°45'N, 175°45'E), Ovrashnii, Bokovoi, Talii, Svetlii and Medveshii Streams, Rarytkin Range, Rarytkin and Koryak Formations, Maastrichtian-Paleocene (Baikovskaya, 1956; Kryshtofovich, 1958b; Golovneva, 1994a, 1994b).
12. Ichvigu-veem River (ca. 64°58'N, 173°59'E), Pekulney Range, Rarytkin Formation, Maastrichtian-Paleocene (Kryshtofovich, 1958a; Golovneva, 1994a, 1994b).
13. Takhobe River (ca. 45°31'N, 137°12'E), Primorye, undefined, Maastrichtian-Paleocene (Baikovskaya, 1956).
14. Lower Amur (ca. 50°56'N, 138°10'E), Primorye, undefined, Maastrichtian-Paleocene (Baikovskaya, 1956).
15. Bureinskaya Tsagayan (49°49'N, 129°50'E), Arkhara (49°28'N, 130°02'E), Raichikha (49°47'N, 129°27'E) and Darmakan River (ca. 49°47'N, 129°21'E), Zee-Bureinskaya Plain, Tsagayan Formation, Maastrichtian-Paleocene (Dorofeev 1951; Sveshnikova 1952, 1963, 1975b; Baikovskaya, 1956; Zamer *et al.* 1963).
16. Snatol River (57°34'N, 157°11'E), western Kamchatka, Napanskya Formation, late Paleocene (Baikovskaya, 1956; Maslova, 2000).
17. Kovachina River (ca. 57°40'N, 158°00'E), Kamchatka Peninsula, undefined, Maastrichtian-Paleocene (Baikovskaya, 1956).
18. Barkinskie clay (53°45'N, 87°12'E), Kuznets Basin, undefined, Maastrichtian-Paleocene (Baikovskaya, 1956).
19. Boguchan River, Amur Valley (49°49'N, 129°50'E), Tsagayan flora, undefined, Paleocene (Kryshtofovich, 1962; Nalivkin, 1973; Krasilov, 1976).
20. Puer Ridge near Malomikhailovka Village (ca. 52°34'N, 140°22'E) on the Amur River, Malomikhailovka Formation, Paleocene (Akhmetiev, 1993; Akhmetiev & Golovneva, 1997).
21. Penjin Bay (63°31'N, 168°00'E), undefined, Eocene (Kryshtofovich, 1958b).
22. Podbazovyi Creek, a tributary of the Taljain River (64°20'N, 175°05'E), Pravotaljainskaya Formation, late Eocene (Akhmetiev & Samsonenko, 1997).

23. Belogolobaya and Duktylikich Rivers south of Ust-Khairyuzovo (57°11'N, 156°45'E), western Kamchatka, Irgirninskaya Formation, late Eocene (Budantsev, 1997).
24. Napana River between Tigil and Sedanka (57°44'N, 158°50'E), western Kamchatka, Russia, Kovachinskaya Formation, late Eocene (Baikovskaya, 1956; Budantsev, 1983, 1997).
25. Irgirnivayam River near Podkagernoye (60°20'N, 161°58'E), western Kamchatka, Russia, Irgirninskaya Formation, late Eocene (Budanstev, 1997).
26. Mainachskii and Tochilinskaya sections near Tigil (58°00'N, 158°10'E), western Kamchatka, Snatol Formation, early Oligocene (Gladenkov *et al.*, 1991).
27. Byeloyarka Village (ca. 57°42'N, 66°08'E), Tavda River, Sverdlovsk region, Nomomikhailovskaya Formation, early Oligocene (Gorbunov, 1962; Dorofeev, 1963a; Sveshnikova, 1963; V.P. Nikitin, personal communication, 2002).
28. Yugan River (ca. 60°40'N, 72°12'E), undefined, ? early Oligocene (Sveshnikova, 1963).
29. Antropovo and Nizhnyaya Pristan Villages (ca. 58°04'N, 65°12'E), Tavda River, Tyumen region, Nomomikhailovskaya Formation, early Oligocene (Dorofeev, 1961, 1963a; Gorbunov, 1962; Zamer *et al.*, 1963; Sveshnikova, 1963; V.P. Nikitin, personal communication, 2002).
30. Tshche-Bas (46°17'N, 59°34'E), Kutanbulak (47°06'N, 61°06'E) and Kenkous (47°09'N, 57°50'E), western Priaralye, Kutanbulakskaya Formation, late Oligocene (Budantsev, 1959; Zhilin, 1974).
31. Kara Chokat near Togyz (47°32'N, 60°32'E), Tashkent Province, Chiliktinskaya Formation, late Oligocene (Uznadze, 1957; Zhilin, 1974).
32. Kumsuat (45°55'N, 58°32'E), western Priaralye, Kutanbulakskaya Formation, late Oligocene (Zhilin, 1974)
33. Lake Khanka (45°00'N, 132°30'E), undefined, Oligocene (Kryshtofovich, 1956).
34. Kuchugui-Kyugelyur River near Khayyr (70°49'N, 133°30'E), Omoloi River Basin, undefined, Oligocene (Dorofeev, 1972).
35. Mt. Ashutas, Lake Zaysan (48°10'N, 84°40'E), undefined, late Oligocene (Kryshtofovich, 1956).
36. Shestakov Log on the left bank of the Bolshaya Kirgizka River 11 km south of Tomsk (56°30'N, 85°05'E), Kasparanskaya Formation, late Oligocene (Gorbunov & Shilkina, 1972).
37. Alexandrovsky and Novy Log (59°10'N, 57°32"E), Visim District, Polevskoi River, Sverdlovsk region, undefined, late Oligocene (Sveshnikova, 1963; Dorofeev, 1970).

38. Section in the southern part of Kvachina Bay near Tigil (58°00’N, 158°10’E), western Kamchatka, Kovachin Formation, late Oligocene (Gladenkov *et al.*, 1991).
39. Section in valley on the Lataevoi River near Ust-Khairyuzovo (57°11’N, 156°45’E), Kamchatka, Kovachin Formation, late Oligocene (Gladenkov *et al.*, 1991).
40. Altyn-Shokysu Tableland, near Aral’sk, Kzyl-Orda District (47°50’N, 60°80’E), Chiliktinskaya Formation, late Oligocene and Aralskaya Formation, early Miocene (Aquitanian) (Zhilin, 1989; Andreyev, 1991).
41. Bukhtarmi River between Rubtsovsk and Aleysk (51°34’N, 81°11’E and 52°32’N, 82°17’E), southern Altai, undefined, late Oligocene-early Miocene (Schmalhausen, 1887; Kornilova, 1966; Rayushkina, 1968, 1979).
42. Kireyev Village (ca. 56°39’N, 84°11’E), Ob River, Tomsk region, undefined, late Oligocene-early Miocene (Dorofeev, 1960, 1963a).
43. Korf Bay (60°18’N, 165°52’E), eastern Kamchatka, Lower Medvezhkinskaya Formation, early Miocene (Chelebaeva, 1971, 1978).
44. Kiniyak (45°29’N, 58°30’E), Mynsualmas (46°06’N, 56°02’E) and Kintykche (45°42’N, 58°31’E), western Priaralye, early Miocene (Zhilin, 1974).
45. Gusinaya River near Penzhino (63°31’N, 168°00’E), Kamchatka, Gusinskoi Formation, Miocene (Ablaev, 1985).
46. Basal layer of the argillaceous tuff, Khasanskaya Hollow near Kraskino (42°42’N, 130°48’E), Primorye, Khasanskaya Formation, early Miocene (Ablaev *et al.*, 1993; Ablaev, 1978; Pimenov, 1990).
47. Right bank of the Dulygaly-Zhilanchik River 4 km north of the Bolattam burial ground (ca. 48°52’N, 65°30’E), Ulutau Region, Karaganda Oblast, undefined, early Miocene (Aquitanian) (Dorofeev, 1963b; Zhilin, 1989).
48. Divide of the Pravaya Granatnaya and Shcherbatovka Rivers near Amgu (45°48’N, 137°36’E), Amgu River Basin, Granatovaya Formation, early to middle Miocene (Klimova, 1981).
49. Southern part of Pavlov section, Primorye, Pavlov Formation, early Miocene (Pimenov, 1990).
50. Prikhankaiskii coal horizon and Chernyshevskaya hollow, Primorye, early and middle Miocene (Pimenov, 1990).
51. Western shore of Lake Khanka (ca. 45°00’N, 132°10’E), Primorye, *Fagus chankaica* layer, undefined, middle Miocene (Pimenov, 1990).
52. Khanka Lake, Primorye (45°00’N, 132°10’E), Khankaiski layer, Botchinskaya Formation, late Miocene (Kryshtofovich, 1946; Baikovskaya, 1974; Ablaev *et al.*, 1994).
53. Mammoth Mountain (63°02’N, 133°17’E), Aldan River, undefined, middle to late Miocene (Dorofeev, 1969).

54. Botchi River near Grossevichi (47°59’N, 139°26’E), Sikhote-Alin, Botchi Formation, late Miocene (Akhmetiev, 1973).
55. Rettikhovka Village (44°10’N, 132°44’E), Primorye, undefined, Miocene (Klimova, 1975; Ablaev, 1978).
56. Zaobsky Yar (56°15’N, 83°57’E), Ob River, undefined, early Pliocene (Gorbunov, 1957, 1962; Zamer *et al.*, 1963).
57. Guria (41°55’N, 42°02’E), Georgia, undefined, Pliocene (Chochieva, 1975).

11.2. Greenland

1. Atanikerdluk (70°04’N, 52°20’W) and Naujât (70°04’N, 52°09’W), Nûgssuaq Peninsula, Upper Atanikerdluk Formation, Quikavsak (Heer’s “Upper Atanikerdluk A” flora) and Naujât (Heer’s “Upper Atanikerdluk B” flora) members, early Paleocene (Heer, 1868, 1870b, 1874, 1883a, 1883b; Koch, 1959, 1963, 1964; Schwarz & Weide, 1962).
2. Agssakak (70°33’N, 51°52’W; syn: Asakak), Nûgssuaq Peninsula, undetermined Tertiary [probably Upper Atanikerdluk Formation, Quikavsak member (Heer’s “Upper Atanikerdluk A” flora), early Paleocene] (Heer, 1874, 1883a, 1883b; Koch, 1963).
3. Qagdlunguaq (70°06’N, 52°25’W; syn: Kardlunguak) NW of Nunguaq, Nûgssuaq Peninsula, Upper Atanikerdluk Formation, Naujât (Heer’s “Upper Atanikerdluk B” flora) member, early Paleocene (Heer, 1883a, 1883b; Koch, 1955; Koch & Pedersen, 1960).
4. Pautût (70°15’N, 52°44’W), Nûgssuaq Peninsula, Upper Atanikerdluk Formation, Quikavsak member (Heer’s “Upper Atanikerdluk A” flora), early Paleocene (Heer, 1883a; Koch 1959, 1963, 1964).
5. Tupaussat (70°19’N, 53°06’W), Nûgssuaq Peninsula, Upper Atanikerdluk Formation, Quikavsak member (Heer’s “Upper Atanikerdluk A” flora), early Paleocene (Koch 1959, 1963, 1964).
6. Agatkløft (70°35’N, 53°07’W), Nûgssuaq Peninsula, Agatdal Formation, Sonja member, early Paleocene (Koch, 1959, 1963, 1964).
7. Qaersutjaegerdal (70°36’N, 53°05’W), Nûgssuaq Peninsula, Agatdal Formation, early Paleocene (Koch, 1959, 1963, 1964).
8. Kangersôk (70°32.5’N, 53°07’W), Nûgssuaq Peninsula, Agatdal Formation, early Paleocene (Koch, 1963, 1964).
9. Sinifik and Puilasok (69°18’N, 53°05’W), Isunguak (69°45’N, 51°55’W), Igdlokungak (69°52’N, 52°21’W) and Ritenbenks Kohlengrube (70°00’N, 53°00’W), Disco Island, Upper Atanikerdluk Formation, Quikavsak member (Heer’s “Upper Atanikerdluk A” flora), early Paleocene (Heer, 1868, 1874, 1883a, 1883b; Koch, 1963).

10. Ingnerit (72°02'N, 55°10'W), Ingnerits Peninsula, undetermined Tertiary, probably Paleocene (Heer, 1883b).
11. Kangiusak (71°44'N, 53°40'W), Svartenbuk Peninsula, undetermined Tertiary, probably Paleocene (Heer, 1883a, 1883b).
12. Prinsesse Thyra Ø (82°00'N, 20°30'W) and Prinsesse Dagmar Ø (81°45'N, 19°00'W), Thyra Ø Formation, late Paleocene-early Eocene (Boyd, 1990).
13. Coal Corner (Christian IV Glacier) near Kangerdlugssuak (78°50'N, 30°50'W), undefined, late Paleocene-early Eocene (Seward & Edwards, 1941; Boulter & Kvaček, 1989).
14. Ivssorrigsok (70°40'N, 54°10'W; syn: Ifsorisok, Qissugssarigsup Qôrua and Kulelv), Nûgssuaq Peninsula, Ifsorisok Formation, late Eocene (Heer, 1874, 1883a, 1883b; Koch, 1959, 1964).
15. Qernertuarssuit (70°48'N, 54°05'W), Nûgssuaq Peninsula, Intrabasaltic, late Eocene (Koch, 1963, 1964).
16. Hareø Island (70°25'N, 54°55'W;syn: Qeqertarssuatsiaq), Intrabasaltic, late Eocene (Heer, 1883a, 1883b; Koch, 1963, 1964).
17. Kugssininguaq (70°35'N, 54°28'W; syn: Kugsinet and Netluarsuk), Nûgssuaq Peninsula, Ifsorisok Formation, late Eocene (Heer, 1874, 1883b; Koch, 1964).

11.3. Spitsbergen/Faroe Island

1. Southwest Ny-Ålesund, Brögger Peninsula (78°55'N, 12°00'W), Spitsbergen, Firkanten Formation, Josephine Coal seam, early Paleocene (Schloemer-Jäger, 1958; Flood *et al.*, 1971; Schweitzer, 1974, Sveshnikova, 1975b; Harland *et al.,*1976).
2. Festningsodden (78°02'N, 14°10'W; syn: Cape Staratschin), Spitsbergen, Firkanten Formation, early Paleocene (Heer, 1870a; Kvacek *et al.*, 1994; Kvaček & Manum, 1997).
3. Kohlenberg (77°47'N, 15°14'W), Bell Sound, Spitsbergen, probably Firkanten Formation, early Paleocene (Heer, 1868; Kvacek *et al.*, 1994).
4. Near Bunessan (56°19'N 6°14'W), Aredtun Peninsula, Isle of Mull, Scotland, Intrabasaltic "leaf beds", late Paleocene (Gardner, 1886; Crane *et al.*, 1988; Boulter & Kvaček, 1989).
5. Mikines (62°07'N, 7°38'W), Faroe Island, undefined, late Paleocene (Rasmussen & Koch, 1963; Boulter & Kvaček, 1989).
6. Nordenskiöldfjellet (Nordenskiölds Berg) and Lars Hiertafjellet (Lars Hjertas Berg) (78°05'N, 15°36'W), Spitsbergen, Aspelintoppen Formation, early Eocene (Kvaček *et al.*, 1994; Kvaček & Manum, 1997).

7. Renardodden (Cape Lyell) and Scottbreen (Scott Gletcher) (77°30'N, 14°30'W), Spitsbergen, Renardodden Formation, late Eocene (Heer, 1876; Schwarz & Weide, 1962; Kvaček *et al.*, 1994).
8. Kaffioyia and Sarsoyra, Forlandsundet Basin (78°40'N, 12°30'W), Spitsbergen, Forlandsundet Formation, late Eocene (Zastawnisk, 1981; Kvaček *et al.*, 1994).

11.4. Arctic Canada

1. Mackenzie River 20 miles above Bear Creek (GSC Loc. 4092 [=1552]) and Near Fort Norman (64°55'N, 125°29'W), Northwest Territory, Brackett Coal Basin, Summit Creek Formation, Paleocene (Heer, 1868, 1880b; Dawson, 1889; Berry 1926a; Bell, 1949; Sweet *et al.*, 1989).
2. Strathcona Fiord (78°38 to 78°40'N, 81°55 to 81°59'W), Ellesmere Island, upper Expedition Formation, early to middle Paleocene and Strand Bay, middle Paleocene (McIver & Basinger, 1999).
3. Fosheim Anticline West (79°34'N, 84°02'W), Ellesmere Island, upper Expedition Formation, early to middle Paleocene (McIver & Basinger, 1999).
4. Fosheim Anticline West (79°43'N, 84°45'W), Ellesmere Island, Lower member, Iceberg Bay Formation, late Paleocene (McIver & Basinger, 1999).
5. Lake Hazen (81°54'N, 69°40'W), Ellesmere Island, Coal member, Iceberg Bay Formation, early Eocene (McIver & Basinger, 1999).
6. Strand Fiord (US163—79°16'N, 91°26'W; US164—79°14'N, 91°26'W; US165–167, US172, US 175–177—79°15'N, 91°16'W; US168–170, 174—79°15'N, 91°10'W; and US178–180—79°14'N, 91°16'W), Axel Heiberg Island, lower member, Iceberg Bay Formation, late Paleocene (McIver & Basinger, 1999).
7. Oxhead Creek (79°43'N, 85°05'W), Mosquito Creek (79°57'N, 84°43'W), Hot Weather Creek (79°56'N, 84°45'W) and Fosheim Peninsula (79°45'N, 85°01'W), Ellesmere Island, Iceberg Bay Formation, late Paleocene-early Eocene (McIver & Basinger, 1999).
8. Stenkul Fiord (77°22'N, 83°28'W), Ellesmere Island, Nunavut, Iceberg Bay Formation, Eureka Sound Group, late Paleocene-early Eocene (Nathorst, 1915; Sveshnikova, 1975a; LePage, unpublished).
9. Strathcona Fiord (78°40'N, 82°40'W), Ellesmere Island, Nunavut, Iceberg Bay Formation, Eureka Sound Group, late Paleocene-early Eocene (LePage, unpublished).
10. Numerous localities throughout the Fosheim Peninsula (ca. 79°40'N, 84°18'W), Ellesmere Island, Nunavut, Iceberg Bay Formation, Eureka Sound Group, late Paleocene-early Eocene (LePage, unpublished).

11. Fort Conger (81°45’N, 64°45’W), Ellesmere Island, Nunavut, probably Iceberg Bay Formation, Eureka Sound Group, late Paleocene-early Eocene (Heer, 1878a).
12. Strathcona Fiord (78°38’N, 82°52.5’W), Stenkul Fiord (77°52’N, 81°38’W) and Split Lake (77°53.2’N, 83°36’W), Ellesmere Island, Margaret Formation, early to middle Eocene (McIver & Basinger, 1999).
13. Napartulik (79°55’N, 89°02’W), Axel Heiberg Island, Nunavut, Buchanan Lake Formation, Eureka Sound Group, middle Eocene (Basinger, 1991).
14. Duck Hawk Bluffs (71°57’N, 125°40’W), Banks Island, Mary Sachs gravels (=Beaufort Formation), middle Miocene (Hills, 1975; Matthews & Ovenden, 1990; Matthews *et al.*, 1986; Matthews, 1987).
15. West River near Horton River (69°12’N, 127°02’W), Northwest Territory, Plateau Cap gravels, middle Miocene (Matthews & Ovenden, 1990).
16. Ballast Brook beds at Ballast Brook (74°19’N, 123°25’W), Banks Island, Canada, unnamed Beaufort Formation equivalent, late Miocene (Heer, 1868; Matthews & Ovenden, 1990; Matthews *et al.*, 1986; Matthews, 1987).
17. Numerous localities on Prince Patrick Island (76–77°N, 116–123°W), Beaufort Formation, early late Pliocene (Matthews & Ovenden, 1990; Matthews *et al.*, 1990).

11.5. Sakhalin

1. Mgachi and Cape Dui (51°03’N, 142°20’E) and Boshnyakovo (49°35’N, 142°12’E), Savayama Formation, early Campanian (Heer, 1878c, 1878d; Kryshtofovich, 1921a; Vakhrameev, 1988).
2. Avgustovka River near Boshnyakovo (49°35’N, 142°12’E), Boshnyakovskaya and Conglomeratovaya Formations, Paleocene (Ablaev, 1978; Krasilov, 1973, 1979).
3. Kamennaya River near Dui (51°03’N, 142°20’E), Conglomeratovaya Formation, Paleocene (Krasilov, 1973; Ablaev, 1978).
4. Kawakami coal mines (=Sinegorsk coal-mine; 47°13’ N; 142°31’E), Anivskiy Region, Naibuchi coal bearing Formation of the Naibuchi Series (=Naibuchinskaya Svita), Eocene (Endo, 1928; Kodrul, 1999).
5. Pilyvo (ca. 50°24’N, 142°14’E) and Borodyazheskaya River (50°35’N, 142°09’E), Conglomerate and Lower Dui Formations, late Eocene-early Oligocene (Borsuk, 1956).

6. Schmidt section (ca. 54°14'N, 142°16'E), Machigarskaya Formation, late Oligocene (Fotyanova, 1988).
7. Khoindzho Promontory near Dui (51°03'N, 142°20'E), Khoindzho Formation, late Oligocene (Fotyanova, 1988).
8. Onnai River near Lesogorsk (49°24'N, 142°10'E), Arakaiskaya Formation, late Oligocene and Kholmsko-Nevefiskaya Formation, early Miocene (Fotyanova, 1988).
9. Shakhtersk Mountain near Shakhtersk (49°11'N, 142°11'E), Naibutinskaya Formation, early Eocene and Shakhterskaya and Verkhneduiskaya Formations, early Miocene (Ablaev, 1978; Fotyanova, 1988).
10. Nadezhdinka River near Lesogorsk (49°24'N, 142°10'E), Shakhterskaya and Verkhneduiskaya Formations, early Miocene (Fotyanova, 1988).
11. Vakhrushev (48°57'N, 142°58'E), Verkhneduiskaya Formation, early Miocene (Pimenov, 1984, 1990; Fotyanova 1988).
12. Korallovka and Gar Rivers near Makarov (48°39'N, 142°45'E), Verkhneduiskaya Formation, early Miocene (Fotyanova, 1988).
13. Novikovo (46°26'N, 143°19'E), Verkhneduiskaya Formation, early Miocene (Fotyanova, 1988).

11.6. China

1. Hunchun, (ca, 43°08'N, 130°04'E) Jilin Province, Hunchun Formation, Senonian (Guo & Li, 1979).
2. Wuyun (49°11'N, 129°08'E), Heilongjinang Province, Wuyun Formation, Wuyun Group, Maastrichtian/Danian (Tao & Xiong, 1986a, 1986b; Liu *et al.*, 1999).
3. Tangyuan (46°30'N, 130°08'E), Heilongjinang Province, Wuyun Formation, Wuyun Group, Maastrichtian/Danian (Zhang *et al.*, 1990).
4. Jiayin (48°40'N, 130°28'E), Heilongjinang Province, Wuyun Formation, Wuyun Group, Paleocene (Lu *et al.,*1983 Xiong, 1986).
5. Yilan coal mine (46°10'N, 129°15'E), Yilan County, Heilongjiang, undefined, early Eocene and early Oligocene (He & Tao, 1994).
6. Fushun coalfield (ca. 41°51'N, 123°53'E) near Shen-yang, Liaoning Province undefined, late Eocene (Endo, 1926, 1928, 1931, 1933b, 1936, 1942; Hu, 1946; Academic Sinica, 1978).
7. Shenbei coalfield (ca. 41°30'N, 123°33'E), Liaoning, Yangliantun Formation, Oligocene (Jin & Shang, 1998).
8. Gaosongshu and Qiuligou Villages (ca. 43°35'N, 128°23'E), Dunhua County, Jilin Province, Tumenzi Formation, early Miocene (Li & Yang, 1984).

9. Taiyang Coal Mining Company 20 km southeast of Taipei (25°05'N, 121°32'E), Shihti Formation, middle Miocene (Canright, 1972).

11.7. Alaska

1. North shore of the Yukon River ca. 12 miles below Melozi telegraph station (ca. 64°44'N, 156°08'W), undivided marine and non-marine sandstones, shales and conglomerate deltaic deposits, Cenomanian/?Turonian (Hollick, 1930; Patton & Moll-Stalcup, 2000).
2. West shore of the Yukon River ca. 17 miles below Nulato (ca. 64°31'N, 158°27'W), undivided marine and non-marine sandstones, shales and conglomerate deltaic deposits, Cenomanian/?Turonian (Hollick, 1930; Patton & Moll-Stalcup, 2000).
3. Coal Creek (syn: Port Moller and Pointe Divide; ca. 55°53'N, 160°47'W), Herendeen Bay, Alaska Peninsula, Chignik Formation, Late Campanian-Early Maastrichtian (Knowlton, 1896; Hollick, 1930, 1936; Detterman *et al.*, 1996).
4. Chignik Bay, Alaska Peninsula (syn: Anchorage Bay; ca. 56°18'N, 158°27'W; USGS Locs. 3519, 3522, 3523), Tolstoi Formation, late Paleocene-early Eocene (Knowlton, 1896; Hollick, 1930, 1936; Wolfe *et al.*, 1966; Detterman *et al.*, 1996).
5. Chignik River below Long Bay (ca. 56°16'N, 158°42'W), Alaska Peninsula, Chignik Formation, Late Campanian-Early Maastrichtian (However, depending upon the exact location, the deposits could also be assigned to the late Paleocene-early Eocene Tolstoi Formation; Hollick, 1930, 1936; Detterman *et al.*, 1996).
6. Sagavanirktok River at Sagwon (69°22.5'N, 148°42'W), Sagavanirktok Formation, Paleocene (Spicer *et al.*, 1994).
7. Numerous localities between 61°38.3'–61°48'N, 147°59.5'–149°05'W (USGS Locs. 5892, 9870–9874, 9877, 9881), Chickaloon Formation, late Paleocene-early Eocene (Martin & Katz, 1912; Hollick, 1936; Wolfe, 1966; Wolfe *et al.*, 1966; Triplehorn *et al.,*1984).
8. Pavlof Bay south of Settlement Point (55°29'N, 161'29'W), Alaska Peninsula, Tolstoi Formation, late Paleocene-early Eocene (Hollick, 1930; Detterman *et al.*, 1996).
9. Ivanof Bay (55°50'N, 159°27'W; USGS Locs. 11411, 11412, 11416), Alaska Peninsula, Tolstoi Formation, late Paleocene-early Eocene (Detterman *et al.*, 1996).
10. Cape Douglas (58°51'N, 153°18'W; USGS Loc. 9761), Copper Lake Formation, early Eocene (Knowlton, 1896; Hollick, 1936; Wolfe *et al.*, 1966; Detterman *et al.*, 1996).

11. Cape Nukshak (syn: Kukak Bay; ca. 58°19'N, 154°01'W), Alaska Peninsula, Hemlock Conglomerate, early Oligocene (Knowlton, 1904; Hollick, 1936; Detterman *et al.*, 1996).
12. Port Camden Bay (56°39'N, 134°02'W), Kuiu Island, Kootznahoo Formation, Angoonian stage, late Oligocene (Heer, 1869; Knowlton, 1896; Hollick, 1936).
13. Head of Hamilton Bay (ca. 56°43.5'N, 133°38'W), Kupreanof Island (USGS Locs. 3652, 4389, 4391, 4392, 7474 and 7565), Kootznahoo Formation, Angoonian stage, late Oligocene (Hollick, 1936; Wolfe *et al.*, 1966; Muffler, 1966).
14. Little Pybus Bay (syn: Murder Cove; 57°15'N, 134°10'W), Admiralty Island, ? Kootznahoo Formation, Angoonian stage, late Oligocene (Loney, 1964; Lathram *et al.*, 1965).
15. Sepphagen mine and De Groff tunnel (ca. 57°35'N, 134°19'W), Kootznahoo Inlet, Admiralty Island, Kootznahoo Formation, Angoonian stage, late Oligocene (Knowlton, 1896; Newberry, 1898; Hollick, 1936).
16. Marvine Glacier, Malaspina District (60°08.8'N, 140°08.25'W; USGS Loc. 11185), Poul Creek Formation, Angoonian stage, late Oligocene (Wolfe, 1977).
17. North shore of Long Island (ca. 57°30'N, 134°20'W; USGS Locs. 9822–9825, 9827), Kootznahoo Inlet, Admiralty Island, Kootznahoo Formation, Angoonian stage, late Oligocene (Wolfe, 1977).
18. Southwest shore of Zarembo Island (56°19'N, 133°14'W), Kootznahoo Formation, Angoonian stage, late Oligocene (Hollick, 1936; Karl *et al.*, 1999).
19. Chicken Creek (64°10'N, 141°58'W; USGS Loc. 10031), ? Kenai Formation, Seldovian stage, early to middle Miocene (Foster, 1969).
20. California Creek (ca. 65°24'N, 150°08'W), probably Usibelli Group, Sanctuary Formation, upper Seldovian stage, middle Miocene (Hollick, 1936; Leopold & Liu, 1994).
21. Mission Creek, (65°11'26"N, 151°57'35"W), probably Usibelli Group, Sanctuary Formation, upper Seldovian stage, middle Miocene (Knowlton, 1898b; Leopold & Liu, 1994).
22. Ninilchik (60°03'N, 151°40'W), Kenai Formation, Clamgulchian stage, early Pliocene (Heer, 1869; Newberry, 1883; Knowlton, 1896; Hollick, 1936; Wolfe, 1966).
23. Chuitna River (61°06'N, 151°09'E; USGS Loc. 9844), Kenai Formation, Homerian stage, early to middle Miocene (Wolfe, 1966).
24. North side of Haenke Glacier (60°6.1'N, 139°11.5'W; USGS Loc. 11183), Yakataga Formation, early middle Miocene (Wolfe, 1977).
25. West side of Tsadaka Canyon (61°42.1'N, 149°05.6'W; USGS Loc. 9359), Kenai Formation, lower Seldovian stage, early to middle Miocene (Wolfe *et al.*, 1966).

26. Little Susitna River (61°41'N, 149°08'W; USGS Loc. 8380), north bank (61°39.4'N, 149°27.8'W; USGS Loc. 9865) and west bank (61°41.7'N, 149°14.7'W; USGS Loc. 9866), Kenai Formation, lower Seldovian stage, early to middle Miocene (Wolfe *et al.*, 1966).
27. Harriet Point (60°33'N, 153°18'W, USGS Locs. 9984 and 9885 and 60°25'N, 152°19'W, USGS Locs. 9886 and 9945) and Redoubt Point (60°18'N, 152°25'W; USGS Locs. 9887 and 9760), Kenai Formation, lower Seldovian stage, early to middle Miocene (Wolfe *et al.*, 1966).
28. North side of the entrance to Chinitna Bay (59°53'N, 152°49'W; USGS Loc. 3505), Kenai Formation, lower Seldovian stage, early to middle Miocene (Hollick, 1936; Wolfe *et al.*, 1966).
29. 0.6 miles south of Point Pogibshi, Seldovia Point (59°25'N, 151°53.1'W; USGS Loc. 9857) and 0.7 miles east of Seldovia Point (59°28.3'N, 151°40.6'W; USGS Loc. 9858), Kenai Formation, upper Seldovian stage, early to middle Miocene (Wolfe *et al.*, 1966; Wolfe & Tanai, 1980).
30. North side of Coal Cove at Port Graham (59°23.7'N, 151°53.7'W; USGS Loc. 9856), Kenai Formation, early to middle Miocene (Heer, 1869; Newberry, 1883; Hollick, 1936; Wolfe, 1966).
31. East bank of Coal Creek at Beluga Lake (61°25.6'N, 151°31.2'W; USGS Loc. 9850), Kenai Formation, upper Seldovian stage, early to middle Miocene (Wolfe *et al.*, 1966).
32. South side of Capp's Glacier (61°18.9'N, 151°46.2'W; USGS Loc. 9845) and west side of high hill (61°16.7'N, 151°45.1'W; USGS Loc. 9846), Kenai Formation, upper Seldovian stage, early to middle Miocene (Wolfe *et al.*, 1966).
33. 1.5 miles above Cache Creek Mining Company's Camp on Cache Creek (62°30'N, 150°57'W; USGS Loc. 6063), Kenai Formation, upper Seldovian stage, early to middle Miocene (Wolfe *et al.*, 1966).
34. South side of Cache Creek (62°29.9'N, 150°56.9'W; USGS Loc. 9868), Kenai Formation, Homerian stage, late Miocene (Wolfe, 1966; Wolfe *et al.*, 1966).
35. South bank of Chuitna River, Cook Inlet (61°07.1'N, 151°18.1'W; USGS Loc. 9844), Kenai Formation, Homerian stage, late Miocene (Wolfe *et al.*, 1966).
36. Chuitna River 0.5 miles south of Old Tyonek, Cook Inlet (61°02'N, 151°17'W; USGS Loc. 4130), Kenai Formation, Homerian stage, late Miocene (Hollick, 1936; Wolfe, 1966; Wolfe *et al.*, 1966).
37. 0.25 miles south of Mutnala Gulch (59°43.2'N, 151°49.4'W; USGS Loc. 9852), Kenai Formation, Homerian stage, late Miocene (Wolfe *et al.*, 1966).
38. Entrance to Troublesome Gulch (59°46'N, 151°51'W; USGS Loc. 4129), Kenai Formation, Homerian stage, late Miocene (Hollick, 1936; Wolfe *et al.*, 1966).

39. 0.25 miles northwest of Diamond Creek (59°40.3’N, 151°42.4’W; USGS Loc. 9366), Kenai Formation, Homerian stage, late Miocene (Wolfe *et al.*, 1966).
40. 1 mile south of Miller’s Landing (59°39.4’N, 151°26.3’W; USGS Loc. 9361), Kenai Formation, Homerian stage, late Miocene (Wolfe *et al.*, 1966).
41. Entrance to Fritz Creek, Kachemak Bay (59°41’N, 151°22’E; USGS Loc. 4131), Kenai Formation, Homerian stage, late Miocene (Hollick, 1936; Wolfe *et al.*, 1966).

11.8. Canada

1. Monkman Pass (54°33’N, 121°15’W; GSC Loc. 3218), British Columbia, Dunvegan Formation, Cenomanian (Bell, 1963).
2. Kistatinaw River (55°51’N, 120°15’W; GSC Loc. 3351), British Columbia, Dunvegan Formation, Cenomanian (Bell, 1963).
3. South Moberly Creek (56°00’N, 121°17’W; GSC Loc. 3618), British Columbia, Dunvegan Formation, Cenomanian (Bell, 1963).
4. East Pine River (55°43’N, 121°13’W; GSC Locs. 4193; 3783 [=3781], 4194, 4197), British Columbia, Dunvegan Formation, Cenomanian (Bell, 1963).
5. North bank of the Kakwa River (54°37’N, 118°27’W; GSC Loc. 5114) about 3 miles below Kapatatik Creek, Alberta, Dunvegan Formation, Cenomanian (Bell, 1963).
6. No. 8 mine dump, Cumberland Coal (1) Ltd. (GSC Loc. 3768), Cumberland (49°37’N, 124°59’W), British Columbia, Comox Formation, Nanaimo Group, Santonian (Bell, 1957, 1962).
7. Port McNeill (50°35’N, 127°06’W; GSC Loc. 3420), British Columbia, undefined Nanaimo Group, Early Campanian (Dawson, 1893; Bell, 1957, 1962).
8. White Rapids Mine (GSC Loc. 3771) and Jingle Pot Mine (GSC Loc. 4210), Nanaimo (49°08’N, 123°58’W), British Columbia, Extension Formation, Nanaimo Group, Early Campanian (Heer, 1865; Dawson, 1882, 1893; Newberry, 1863, 1898; Bell, 1957, 1962; Chaney, 1951).
9. Protection (49°11’N, 123°55’W; GSC Locs. 1580, 3858) and Round (GSC Loc. 3826) Islands, British Columbia, Protection Formation, Nanaimo Group, Late Campanian (Dawson, 1882; Clapp, 1914; Bell, 1957, 1962).
10. Cutbank Creek (53°20’N, 113°53’W; GSC Loc. 3671 [=3669]) 3 miles south of Theresa on the Nose Mountain Trail, Alberta, Wapiti Group, Late Cretaceous (Bell, 1949).

11. Lower reaches of Reynolds Creek along the Great Pacific Railway, near the Parsnip River (54°56’N, 122°39’W), British Columbia, Sustut Group, ? Sifton Formation, Late Cretaceous-early Paleocene (Rouse, 1967).
12. Ravenscrag Butte near Ravenscrag (49°30.4’N, 109°1.2’W), Saskatchewan, Ravenscrag Formation, Paleocene (McIver & Basinger, 1993).
13. Genesee (53°21’N, 114°24’W), Alberta, Scollard member, Paskapoo Formation, Paleocene (Chandrasekharam, 1974).
14. Alexo (52°27’N, 115°48’W; GSC Loc. 3428), Alberta, probably Scollard member, Paskapoo Formation, Paleocene (Bell, 1949).
15. Short Creek (GSC Loc. 1651), Souris River near Roche Percée (49°04’N, 102°48’W), Saskatchewan, Ravenscrag Formation, Paleocene (Dawson, 1881, 1887; Penhallow, 1903; Bell, 1949).
16. Willow Creek (50°10’N, 113°50’W; GSC Loc. 3700), Alberta, Willow Creek Formation, Ravenscrag Formation, Paleocene (Bell, 1949).
17. Lamoral (52°26’N, 115°30’W), Clearwater County, Alberta, Paskapoo Formation, Paleocene (Penhallow, 1903; Allan & Rutherford, 1926; Berry, 1926b).
18. Near Niven River and Thutade Lake (56°56’N, 126°55’W; GSC Locs. 3487, 3488, 3489), British Columbia, Sustut Group, Paleocene (Lord, 1948; Bell, 1949).
19. 2 miles north of François Lake (56°02’N, 125°38’W; GSC Locs. 4072, 3013, 1770), British Columbia, Sustut Group, Paleocene (Armstrong, 1949).
20. 1 mile north of the mouth of T-Allin Creek (56°02’N, 125°58’W; GSC Loc. 4084), British Columbia, Sustut Group, Paleocene (Armstrong, 1949).
21. Ed Bird and Estella Lakes (56°57’N, 125°05’W), British Columbia, Sustut Group, Sifton Formation, Paleocene (Roots, 1954).
22. 6.5 miles southeast of the mouth of the Rapid River (59°10’N, 128°55’W; GSC Loc. 4235), British Columbia, Rapid Formation, Paleocene (Gabrielse, 1963).
23. Fish and Pedley Creeks (53°26’N, 117°36’W), Alberta, Paskapoo Formation, Paleocene (Lang, 1947).
24. Southeast of Goodlands (49°01’N, 100°32’W), Manitoba, Turtle Mountain Formation, Paleocene (Wickenden, 1945).
25. Munce’s Hill 3 km northeast of Canyon Ski Quarry and Gao Mine locality (roadcut on the north bank of Highway 593, 14 km east of Red Deer [52°15’N, 113°48’W]) near Red Deer, Alberta, Paskapoo Formation, Paleocene (late Tiffanian Ti_4) (Falder *et al.,*1999).
26. 12 miles east of Ponoka (52°42’N, 113°24’W) and 9 miles east of Red Deer (52°15’N, 113°41’W), Alberta, Paskapoo Formation, Paleocene (Allan & Rutherford, 1926; Berry, 1926b).

27. Porcupine Creek (= Poplar River) west of Maxstone (ca. 49°28’N, 106°02’W) and north of Twelve Mile Lake, Saskatchewan, Ravenscrag Formation, Paleocene (Dawson, 1875; Penhallow, 1903, 1907b, 1908; Berry, 1926a, 1930, 1935; Williams & Dyer, 1930).
28. 3.5 miles east of Ravenscrag (49°30’N, 109°08’W), Saskatchewan, Ravenscrag Formation, Paleocene (Williams & Dyer, 1930).
29. Approximately 10 miles southeast of Willowbunch (49°22’N, 105°39’W), Saskatchewan, Ravenscrag Formation, Paleocene (Berry, 1935; Williams & Dyer, 1930).
30. Approximately 10 to 15 miles southwest of Bengough (49°25’N, 105°10’W), Saskatchewan, Ravenscrag Formation, Paleocene (Berry, 1935; Williams & Dyer, 1930).
31. Approximately 5 miles south of Big Muddy Lake (49°09’N, 105°00’W), Saskatchewan, Ravenscrag Formation, Paleocene (Berry, 1935; Williams & Dyer, 1930).
32. Kneehills Creek on left bank of the Red Deer River (57°30’N, 112°50’W), Edmonton Formation, Paleocene (Williams & Dyer, 1930).
33. Mouth of the Blind Man River (52°22’00”N, 113°46’05”W), Red Deer River Valley, Paskapoo Formation, Paleocene (Penhallow, 1902, 1903, 1906; Allan & Rutherford, 1926; Berry, 1926a).
34. 80 miles SE of Grand Prairie (54°15’N, 118°45’W, Smokey Tower, Alberta, Volcanic Tuff flora, Paleocene (Christophel, 1974).
35. Diamond Vale Coal Company, Quilchena near Nicola (50°08’N, 120°31’W), British Columbia, Kamloops Group, Coldwater beds, middle Eocene (Penhallow, 1906, 1908; Berry, 1926a; Armentrout, 1981; Mathewes & Brooke, 1971).
36. Tranquille River near Kamloops (50°39’N, 120°24’W), British Columbia, Canada, Kamloops Group middle Eocene (Penhallow, 1908; Berry, 1926a).
37. Joseph Creek (51°28’N, 120°08’W; GSC Loc. 7070), British Columbia, Chu Chua Formation, middle Eocene (Berry, 1926a; Campbell & Tipper, 1971; Roddick *et al.*, 1976; Armentrout, 1981).
38. Ashnola locality (49°22.7’N, 120°32.7’W) near Princeton, British Columbia, Allenby Formation, middle Eocene (Arnold, 1955; Hills & Baadsgaard, 1967; Rothwell & Basinger, 1979; Basinger, 1981, 1984).
39. 2 to 2.5 miles south of Cache Creek and 4 miles east of Cache Creek (50°50’N, 121°10’W), British Columbia, Coldwater beds, early middle Eocene (Duffell & McTaggart, 1952).
40. 2.5 miles south of Sihwe Creek (50°25’N, 121°43’W), British Columbia, Kamploops Group, middle Eocene (Duffell & McTaggart, 1952).
41. Newhykulston Creek (51°18’N, 120°09’W; GSC Loc. 7069), British Columbia, Chu Chua Formation, middle Eocene (Campbell & Tipper, 1971).

42. Brewery Creek near Stikine River (57°48'N, 131°25'W), British Columbia, undefined, Eocene (Kerr, 1948).
43. Whipsaw and Lamont Creeks (49°23'N, 120°34'W), British Columbia, Princeton Group, Allenby Formation, middle Eocene (Rice, 1947).
44. Vermilion Cliff on the Tulameen River 3 miles west of Princeton (49°27'N, 120°34'W), British Columbia, Princeton Group, Allenby Formation, middle Eocene (Penhallow, 1908; Berry, 1926a; Rice, 1947).
45. Kettle River just north of the US-Canada border approximately 6 miles upstream from Midway (49°02'N, 118°45'W), British Columbia, probably Princeton Group, Allenby Formation, middle Eocene (Penhallow, 1907a, 1908).
46. Nine-mile Creek (49°26'N, 120°18'W), British Columbia, probably Princeton Group, Allenby Formation, middle Eocene (Dawson, 1879).
47. Similkameen River near Princeton (49°25'N, 120°35'W), British Columbia, middle Eocene (Dawson, 1891; Penhallow, 1903, 1908; Berry, 1926a; Armentrout, 1981).
48. Coal Gully near Coutlee (50°08'N, 120°49'W), British Columbia, Kamloops Group, Coldwater beds, middle Eocene (Penhallow, 1906).
49. Miocene Mines, Horsefly River near Horsefly (52°20'N, 121°25'W), British Columbia, Horsefly River beds, middle Eocene (Penhallow, 1902, 1903, 1908; Berry, 1926a; Wilson, 1977).
50. Kitsilano (49°16'N 123.10'W), south side of English Bay, Vancouver, British Columbia, Kitsilano Formation, late Eocene-early Oligocene (Johnson, 1923; Berry, 1926a; Chaney, 1951).
51. 2.6 miles west of the Devil's Thumb (53°35'N, 125°20'W), British Columbia, Endako Group, late Oligocene (Tipper, 1963).
52. West Road (= Blackwater) River (53°19'N, 122°52'W), British Columbia, probably Endako Group, late Oligocene (Dawson, 1877; Penhallow, 1908; Berry, 1926a).
53. Deadman River Valley south of Snohoosh Lake (51°03'N, 120°53'W; GSC Loc. 7067), British Columbia, Deadman Formation, late Miocene (Campbell & Tipper, 1971).

11.9. USA

1. Red Coulée (47°33'N, 110°57'W), Cascade County, Montana, Eagle Sandstone, late Santonian-early Campanian (Bell, 1963).
2. Hunter Wash (36°17N, 108°15'W), 30 miles south of Farmington and 1 mile east of the Reservation line, San Juan County, New Mexico, Fruitland Formation, late Campanian (Knowlton, 1917a).

3. SE 1/4, S. 6, T. 49 N, R. 99 W (44°15'N, 108°48'W; USGS Loc. 6176), Park County, Wyoming, Ferris Formation, Late Cretaceous-early Paleocene (Brown, 1962).
4. Rattlesnake Butte (45°16'31"N, 107°40'08"W), Cheyenne Indian Reservation, Bighorn County, South Dakota, Lance Formation, late Maastrichtian (Knowlton, 1911).
5. Near Lance Creek (43°22'N, 104°16'W), Niobrara County, Wyoming, Lance Formation, late Maastrichtian (Dorf, 1940, 1942).
6. Craig (40°31'N, 107°33'W), Moffat County, Colorado, Medicine Bow Formation, late Maastrichtian (Dorf, 1942).
7. Oakdale mine, northwest of La Veta (37°30'N, 105°00'W), Huerfano County, Colorado, Vermejo Formation, late Maastrichtian (Knowlton, 1917b).
8. McAinlly mine near Walsenburg (37°37'N, 104°46'W), Huerfano County, Colorado, Vermejo Formation, late Maastrichtian (Knowlton, 1917b).
9. Starkville mine, Starkville, (37°07'N, 104°31'W), Las Animas County, Colorado, Vermejo Formation, late Maastrichtian (Knowlton, 1917b).
10. Morley mine, Morley (37°02'N, 104°30'W), Las Animas County, Colorado, Vermejo Formation, late Maastrichtian (Knowlton, 1917b).
11. Vermejo Park (36°53'N, 105°00'W), Colfax County, New Mexico, Vermejo Formation, late Maastrichtian (Knowlton, 1917b).
12. Dawson (36°40'N, 104°46'W), Colfax County, New Mexico, Vermejo Formation, late Maastrichtian (Knowlton, 1917b).
13. Ponil Creek (36°28'N, 104°47'W), Colfax County, New Mexico, Vermejo Formation, late Maastrichtian (Knowlton, 1917b).
14. Bug Creek Anthills near the Fort Peck Reservoir (47°40'N, 106°13'W), McCone County, Montana, Hell Creek Formation, late Maastrichtian (Shoemaker, 1966).
15. Cannonball River 30 miles south of Mandan (46°24'N, 100°53'W), Morton County, North Dakota, Lance Formation, late Maastrichtian (Brown, 1935a).
16. Marmarth (46°17'N, 103°55'W), Slope County, North Dakota, Hell Creek Formation, late Maastrichtian (Brown, 1939; Chaney, 1951).
17. No. 6 mine, Forbes (37°15'23"N, 104°33'47"W), Las Animas County, Colorado, Vermejo Formation, late Maastrichtian (Knowlton, 1917b).
18. Willow Creek ca. 12 miles north of Musselshell Post Office and 1 mile east of road from Junction City to Fort Maginnis (46°41'N, 108°01'W), Fergus County, Montana, ?Judith River Formation, Maastrichtian (Knowlton, 1905).
19. Custro in Tercio Park (37°03'N, 104°59'W), Las Animas County, Colorado, Vermejo Formation, late Maastrichtian (Knowlton, 1917b).

20. S. 31, T. 50 N, R. 99 W (44°16'N, 108°48'W; USGS Loc. 6173), Park County, Wyoming, Ferris Formation, Late Cretaceous-early Paleocene (Brown, 1962).
21. Sand Creek, 7 miles north of Glenrock (42°58'N, 105°51'W; USGS Loc. 8551), Converse County, Wyoming, Fort Union Formation, early Paleocene (Brown, 1962).
22. Bluffs on the west side of the Little Missouri River, 2 miles south of Medora (46°53'N, 103°37'W; USGS Loc. 4264), Billings County, North Dakota, Fort Union Formation, early Paleocene (Brown, 1962).
23. Near the top of Sentinel Butte (46°52'N, 103°50'W; USGS Loc. 8238), Golden Valley County, North Dakota, Fort Union Formation, early Paleocene (Brown, 1962).
24. 3 miles SW of Yule (46°32'N, 103°49'W; USGS Loc. 8240), Golden Valley County, North Dakota, Fort Union Formation, early Paleocene (Knowlton, 1909; Brown, 1962).
25. 6.5 km north of New Salem (46°54'N, 101°25'W), Morton County, North Dakota, Fort Union Formation, early Paleocene (Harr & Ting, 1976).
26. Road cut east-southeast of Medora (46°55'N, 103°32'W), Billings County, North Dakota, Fort Union Formation, early Paleocene (Harr & Ting, 1976).
27. S. 33, T. 37 N, R. 47 E (47°22'N, 104°23'W; USGS Loc. 7005), left bank of the Yellowstone River at Burns, Richland County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).
28. 30 miles below Gendive (46°41'N, 104°44'W; USGS Loc. 2420), Dawson County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).
29. SW 1/4, NW 1/4, S. 28, T. 31N, R. 19 E, S of Chinook (48°34'N, 109°13'W; USGS Loc. 5595), Blaine County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).
30. 10 miles N of Terry in S. 19, T. 13 N, R. 50 E (46°56'N, 105°19'W; USGS Loc. 8556), Prairie County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).
31. SW 1/4, S. 27, T. 5 S, R. 50 E, about 6 miles SW of Broadus (45°24'N, 105°28'W; USGS Loc. 8786), Powder River County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).
32. Makton coal mine, 7 miles NE of Big Sandy (48°13'N, 109°58'W; USGS Loc. 8885), Chouteau County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).
33. 2 miles SW of Edwards (47°07'N, 107°22'W USGS Loc. 8249), Garfield County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).
34. East side of Smokey Butte Creek, 14 miles NW of Jordan (47°24'N, 107°10'W; USGS Loc. 9334), Garfield County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).

35. Klonders Ranch 18 miles NE of Miles City (46°35’N, 105°33’W; USGS Loc. 8550), Montana, Fort Union Formation, early Paleocene (Knowlton, 1909; Brown, 1962).
36. 8 miles west of Bridger (45°20’N, 109°01’W), Carbon County, Montana, Fort Union Formation, early Paleocene (Knowlton, 1909).
37. Signal Butte 5 miles east of Miles City (46°23’N, 105°45’W), Custer County, Montana, Fort Union Formation, early Paleocene (Knowlton, 1909).
38. Whetstone Falls, on a tributary of Pacific Creek NE of Moran (43°50’24”N, 110°30’34”W; USGS Loc. 9193), Teton County, Wyoming, Fort Union Formation, early Paleocene (Brown, 1962).
39. Bud Kimball Mine (44°00’N, 107°32’W; USGS Loc. 5063), Washakie County, Wyoming, Fort Union Formation, early Paleocene (Knowlton, 1909; Brown, 1962).
40. SW 1/4, S. 5, T. 45 N, R. 97 W (43°54’N, 108°31’W), Hot Springs County, Wyoming, Fort Union Formation, early Paleocene (Brown, 1962).
41. South Park (43°25’N, 110°47’W), Teton County, Wyoming, Fort Union Formation, early Paleocene (Lesquereux, 1874).
42. Ilo and Gynne Ranch near Grass Creek (43°56’25”N, 108°38’55”W; USGS Locs. 4661, 8899), Hot Springs County, Wyoming, Fort Union Formation, early Paleocene (Knowlton, 1909; Brown, 1962).
43. Little Missouri River, near New Town (syn: Elbowoods; 47°58’54”N, 102°30’49”W Fort Berthold Reservation; USGS Loc. 8212), Mountrail County, North Dakota, Fort Union Formation, early Paleocene (Brown, 1962).
44. Roadcut ESE of Medora (46°51’30”N, 103°25’02”W), Billings County, North Dakota, Fort Union Formation, early Paleocene (Harr & Ting, 1976).
45. 6.5 km north of New Salem (46°54’N, 101°26’W), Morton County, North Dakota, Fort Union Formation, early Paleocene (Harr & Ting, 1976).
46. 3 miles NW of Meeteetse (Black Diamond Mine; ca. 44°11’N, 108°55’W), Park County, Wyoming, Fort Union Formation, early Paleocene (Knowlton, 1909).
47. Shoshone River near Cody (44°32’N, 109°03’W), Park County, Wyoming, Fort Union Formation, early Paleocene (Knowlton, 1909).
48. *Ceratops* beds along Lance Creek (43°14’N, 104°36’W), Converse County, Wyoming, Fort Union Formation, early Paleocene (Knowlton, 1909).
49. Seven Mile Creek (43°23’52”N, 104°25’05”W), Niobrara County, Wyoming, Fort Union Formation, early Paleocene (Knowlton, 1909).
50. SW 1/4, S. 15, T. 15 N, R. 47 E (47°03’10”N, 105°45’56”W; USGS Loc. 8165), Prairie County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).

51. Bison Basin (42°16’31”N, 108°05’58”W), Fremont County, Wyoming, Fort Union Formation, early Paleocene (Gemmill & Johnson, 1997).
52. S. 34, T. 6N, R. 27 E, 6 miles E of Buckley (46°13’44”N, 108°19’50”W; USGS Loc. 4582), Yellowstone County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).
53. NE 1/4, SW 1/4, S. 23, T. 5 N, R. 26 E, 2 miles south of Buckley (46°10’20”N, 108°26’01”W; USGS Loc. 4984), Musselshell County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).
54. Point of Rocks (41°41’N, 108°47’W), Sweetwater County, Wyoming, Fort Union Formation, early Paleocene (Lesquereux, 1876; Knowlton, 1900a; Chaney, 1951).
55. Near the top of a conical hill, S. 23, T. 2 S, R. 44 E (43°39’22”N, 106°15’45”W; USGS Loc. 8521), Rosebud County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).
56. Twisp (48°22’N, 120°07’W), Okanogan County, Washington, Pipestone Formation, Paleocene (Royse, 1965).
57. Route 719 across from the S. 24, T. 143 N, R. 101 W, (47°11’30”N, 103°25’26”W), Billings County, North Dakota, Fort Union Formation, early Paleocene (Harr & Ting, 1976).
58. Carbon (41°51’N, 106°22’W), Carbon County, Wyoming, Fort Union Formation, early Paleocene (Lesquereux, 1873).
59. Farley Creek (44°56’N, 107°08’W) about 2 1/4 miles NE of Ranchester, Sheridan County, Wyoming, Fort Union Formation, early Paleocene (Knowlton, 1909).
60. East side of Bighorn River across from Kirby (43°48’N, 108°10’W), Hot Springs County, Wyoming, Fort Union Formation, early Paleocene (Knowlton, 1909).
61. Rock Springs (41°35’N, 109°12’W), Sweetwater County, Wyoming, Fort Union Formation, early Paleocene (Chaney, 1951).
62. Hodson’s coal mine on Meadow Creek (45° 38’N, 110°52’W), 12 miles SE of Bozeman, Gallatin County, Montana, Fort Union Formation, early Paleocene (Knowlton, 1893b).
63. Big Dry Creek (47°30’55”N, 106°16’41”W), ca. 60 miles south of Glasgow, McCone County, Montana, Fort Union Formation, early Paleocene (Knowlton, 1909).
64. 6 miles above the mouth of Sevenmile Creek NE of Glendive (47°06’23”N, 104°42’39”W; USGS Loc. 8196), Dawson County, Montana, Fort Union Formation, early Paleocene (Brown, 1962).
65. Yellowstone River near O’Fallon’s Creek (46°50’11”N, 105°08’50”W), Prairie County, Montana Fort Union Formation, early Paleocene (Newberry, 1868, 1898; Chaney, 1951).

66. Lone Butte (47°30’09”N, 103°09’30”W), McKenzie County, North Dakota, Sentinel Butte mudstone, Sentinel Butte Formation, Paleocene (Hoganson, 1997).
67. Medicine Lodge (Sage) Creek (44°59’N, 112°57’W), Beaverhead County, Montana, unknown, probably Paleocene (Lesquereux 1872; Knowlton 1923; Chaney 1951).
68. Numerous localities in Mountrail, Dunn, Mercer, Morton, McKenzie and Stark Counties (between ca. 46°30’N to 48°00’N, 101°30’W to 103°30’W; USNM Locs. 14056, 14059, 14066, 14068, 14074, 14079, 14083, 14085, 14088, 14098, 14108, 14115, 14121, 14122, 14128 and 14142), North Dakota, Bear Den and Camel Butte members, Golden Valley Formation, late Paleocene-early Eocene (Hickey, 1977).
69. SE 1/4, NW 1/4, S. 28, T. 9 N, R. 80 W, 7 miles west of Walden (40°44’N, 106°25’W; USGS Loc. 6000), Jackson County, Colorado, Coalmont Formation, late Paleocene-early Eocene (Brown, 1962; Roberts & Rossi, 1999).
70. Beckler Creek and Foss River Valley (ca. 47°42’N, 121°19’W), Skykomish Basin, Washington, Swauk Formation, late Paleocene-early Eocene (Smith & Duror, 1916).
71. Elko Station (40°50’N, 115°46’W), Elko County, Nevada, Elko Formation, early Eocene (Lesquereux, 1873, 1874; Chaney, 1951; Wing, 1987).
72. Pleasant Bay, SE 1/4 of SE 1/4 section 25, T. 37 N, R 2E (48°39’53”N, 122°29’48”W), Whatcom County, Washington, Chuckanut Formation, early Eocene (Pabst, 1968).
73. Birch Bay (48°55’N, 122°44’W), Whatcom County, Washington, Chuckanut Formation, early Eocene (Newberry, 1863, 1898; Chaney, 1951).
74. Chuckanut Drive on State highway 99A about 1/2 mile northwest of Dogfish Point, Clayton Bay, SE 1/4 of SW 1/4 section 6, T. 36 N, R 2E (48°37’32”N, 122°27’45”W), Skagit County, Washington, Chuckanut Formation, early Eocene (Pabst, 1968).
75. Germer Basin (44°30’N, 114°14’W), Custer County, Idaho, Germer Tuffaceous Member, Challis Volcanics, middle Eocene (Edelman, 1975).
76. Republic (48°39’N, 118°45’W), Ferry County, Washington, Klondike Mountain Formation, middle Eocene (Brown, 1935b; Wolfe & Wehr, 1987).
77. Bear Creek near Pinson (35°30’N, 88°45’W), Madison County, Tennessee, Lagrange Formation, late Eocene (Berry, 1916).
78. South end of the Ruby Reservoir between Mormon and Peterson Creeks (45°12’N, 112°09’W), Ruby Basin, Madison County, Montana, Renova Formation, late Eocene (Becker, 1960, 1961; Armentrout, 1981; Call & Dilcher, 1997).

79. Grant (45°00’N, 113°04’W), Beaverhead County, Montana, Medicine Lodge florule, Beaverhead Basin, Renova Formation, late Eocene (Becker, 1969; Call & Dilcher, 1997).
80. Fossil (45°01’N, 120°11’W), Cove Creek (syn: Knox Ranch and Pentecost Ranch; 44°54’N, 120°23’W) and Iron Mountain (syn: Clarno’s Ferry, Chapman Ranch, Dugout Gulch and Slanting leaf beds; 44°41’N, 119°54’W), Wheeler County, Oregon, western facies of the Bridge Creek flora, John Day Formation, early Oligocene (Knowlton, 1902; Mason, 1927; Chaney, 1951; Manchester & Meyer, 1987; Meyer & Manchester, 1997).
81. Twickenham (44°45’N, 120°14’W) and Painted Hills (syn: Allen Ranch, Bridge Creek [*sensu sticto*], Mitchell and Wade Ranch; 44°38’N, 120°17’W), Wheeler County, Oregon, eastern facies of the Bridge Creek flora, John Day Formation, early Oligocene (Lesquereux, 1883; Newberry, 1883, 1898; Knowlton, 1902; Chaney, 1951; Arnold, 1952; Brown, 1959; Meyer & Manchester, 1997).
82. Lost Creek (syn: Post and Gray’s Ranch; 44°38’N, 120°17’W) and Crooked River (syn: Gray’s Ranch and Post; 44°09’N, 120°19’W), Crook County, Oregon, southern facies of the Bridge Creek flora, John Day Formation, early Oligocene (Newberry, 1898; Chaney, 1927; Mason, 1927; Clements & Chaney, 1936; Arnold, 1947; Chaney, 1951; Meyer & Manchester, 1997).
83. Canal flora near Redmond (44°15’N, 121°11’W), Deschutes County, Oregon, Clarno Formation, middle Oligocene (Ashwill, 1983).
84. 0.8 miles NE of Rujada and 23 miles E of Cottage Grove (43°48’N, 122°35’W), Lane County, Oregon, late Oligocene (Lakhanpal, 1958).
85. Thomas Creek 5 miles southeast of Lyons (44°41’N, 122°31’W), Linn County, Oregon, Little Butte Volcanic Series, Oligocene (Meyer, 1973).
86. Franklin Butte (44°30’N, 122°30’E) near Scio, Linn County, Oregon, Little Butte Volcanic Series, Oligocene (Sanborn, 1949).
87. Hay Fork (40°33’N, 123°13’W), Shock Creek (40°34’35”N, 123°02’33”W), Redding Creek (40°35’N, 123°53’W), Big Bar (40°44’31”N, 123°15’03”W) and Hyampom (40°37’N, 123°27’W), Trinity County, California, Weaverville Formation, Oligocene (MacGinitie, 1937).
88. Warner Mountains (ca. 41°32’N, 120°10’W), Modoc County, California, Lower Cedarville Formation, late Oligocene-early Miocene (Russell, 1928; Chaney 1951).
89. *Metasequoia* Creek on the Columbia River (45°37’12”N, 121°59’13”W), Oregon, Eagle Creek Formation, early Miocene (Krause, 1999).
90. Electric powerhouse on the right bank of the Salmon River near Salmon (45°10’N, 113°53’W), Lemhi County, Idaho, early Miocene (Brown, 1935b; Chaney, 1951).

91. Left side of the road up Potlatch Creek between Arrow Junction and Juliaetta (ca. 46°32’N, 116°43’W), Latah County, Idaho middle Miocene (Brown, 1935b).
92. Good Hope Hill (38°52’04”N, 76°57’45”W), Anacostia River, District of Columbia, Calvert Formation, Miocene (Berry, 1909).
93. 1 mile east of Murphy’s Springs and about 4 miles southeast of Ashland (42°10’N, 122°47’W), 3 miles south east of Ashland (42°10’N, 122°45’W) and 5 miles north of Ashland (42°16’N, 122°43’W), Jackson County, Oregon, undefined, Miocene (Knowlton, 1900b; Chaney, 1951).
94. Hog and Alkali Creeks near Weiser (44°15’N, 116°58’W), Washington County, Idaho, Idaho Formation, late Miocene/early Pliocene (Dorf, 1936; Smith, 1938).
95. Clarkia (47°00’N, 116°15’W), Shoshone County, Idaho, Miocene (Smiley *et al*., 1975; Smiley & Rember, 1985).
96. Picture Gorge (44°31’51”N, 119°38’03”W) to White Hills locality (syn: Van Horn’s Ranch or Belshaw Ranch; ca. 44°25’N, 119°14’W) along the east fork of the John Day River, Grant County, Oregon, John Day Formation, early Oligocene, (Knowlton, 1902; Cockerell, 1910; Chaney & Axelrod, 1959; Chaney, 1951).
97. 3.5 miles south of Lone Rock (ca. 44°13’N, 118°15’W), Oregon, John Day Formation, early Oligocene (Knowlton, 1902).
98. Edward’s Ranch, Stanley Hill near Coeur D’Alene (47°40’N, 116°47’W), Kootenai County, Idaho, Latah Formation, middle Miocene (Knowlton, 1926).
99. $\frac{1}{2}$ mile above the mouth of Deep Creek (47°45’N, 117°33’W) northwest of Spokane, Spokane County, Washington, Latah Formation, middle Miocene (Knowlton, 1926).
100. Well at Mica (47°33’N, 117°12’W) ca. 10 miles SE of Spokane, Spokane County, Washington, Latah Formation, middle Miocene (Knowlton, 1926).
101. Cut along the Spokane, Portland and Seattle Railway, Spokane (47°39’N, 117°25’W), Spokane County, Washington, Latah Formation, middle Miocene (Knowlton, 1926).
102. Cut ca. 1 miles west of Shelley Lake (47°39’N, 117°12’W) about 10 miles east of Spokane, Washington, Latah Formation, middle Miocene (Knowlton, 1926).

11.10. Korea

1. Keumkwandong near Pohang (36°00’N, 129°36’E), Yeong’il Bay District, Changgi flora, Keumkwandong Formation, Changgi Group, early Miocene (Huzioka, 1972; Chun, 1982).

2. Ung'jeomdong near Yongdong and Myeoncheon ca. 30 northeast of Kilju (40°55'N, 129°21'E), Myeoncheon-Kilju District, Yongdong flora, Yongdong Formation, Yongdong Group, early Miocene (Huzioka, 1972).
3. Tongcheon coal field (Tsusen coal field, Kogen-do; ca. 38°41'N, 128°10'E), Tongcheon District, Kangweon-do, Tongcheon flora, Tongcheon Formation, late early to early middle Miocene (Ichimura, 1928; Endo, 1938b, 1939; Huzioka, 1972).
4. Hamjindong (Kantindô and Hakurokudô (Hugandô) coal mines) and Kilju (40°55'N, 129°21'E), Myeoncheon-Kilju District, Hamjindong flora, Hamjindong Formation, Myeoncheon Group, middle Miocene (Endo, 1936, 1938a, 1939; Huzioka, 1972).
5. Yongpukdong in the Kogeonweon coal field (Kokangen coal mine) located about 40 km northeast of Hoeryeong (42°29'N, 129°45'E), Kyeongweon District of Hamg'yeong-bukdo, Kogeonweon flora, "*Engelhardtia* bed", middle Miocene (Endo, 1938a, 1939; Huzioka, 1972).
6. Aojidong coal field located about 40 km northeast of Hoeryeong (42°29'N, 129°45'E), Kyeongweon District of Hamg'yeong-bukdo, Kogeonweon flora, lower coal-bearing bed, middle Miocene (Endo, 1938a; Huzioka, 1972).
7. Kungshim colliery at Kungshimdong 7.5 km northeast of Hoeryeong (42°29'N, 129°45'E), Hoeryeong District, Kungshim flora, Hoengyeong Formation, early middle Miocene (Ichimura, 1927; Huzioka, 1972).
8. Paektodong located about 10 km southwest of Hoeryeong (42°29'N, 129°45'E), Hoeryeong District, Kungshim flora, Yuseon Formation, early late Miocene (Ichimura, 1927; Huzioka, 1972).

11.11. Japan

11.11.1. Hokkaido

1. Owada coal mines near Rumoi City (43°55'N, 141°38'E), Rumoe District, Tesio, Yudoro Formation, late Eocene (Endo, 1936; Oishi, 1950; Tanai, 1955).
2. Shimizusawa coal mine, Ishikari coal field near Yubari City (43°20'N, 142°10'N), Yubari District, Yubari Formation, Eocene (Endo, 1928; Huzioka & Kobayashi, 1961).
3. Shako and Sarushihorokabetsu, Yubari City (43°11'N, 142°00'E), and Tekkonosawa, Kuriyama-machi, Sarachi District, Ishikari coal field, *Woodwardia* Formation, middle Eocene (Endo, 1968).
4. Kushiro coalfield near Kushiro City (43°10'N, 145°10'E), Harutori, Tenneru, Shakubetsu and Yubetsu Formations, Urahoro Group, late Oligocene (Oishi & Huzioka, 1942; Tanai, 1970; Matsue & Onoe, 1995).

5. Ponbetsu coal mine, near Mikasa City (43°15'N, 141°57'E), Fukagawa-machi, Sorachi District, Naidabu Formation, early to middle Miocene (Endo, 1928; Tanai, 1955).
6. Near Kanasagawa and Miyano (42°20'N, 139°56'E), Wakamatsu flora, Sekinai Formation, middle Miocene (Tanai & Suzuki, 1972).
7. Kayanuma coal mine on the upper course of the Tama River near Kayanuma north of Iwani (43°01'N, 140°32'E), Fukuyama Formation, Miocene (Tanai, 1955, 1961; Tanai & Suzuki, 1963).
8. Yoshioka flora near Yoshioka (41°26'N, 140°54'E), Yoshioka Formation, late early to early middle Miocene (Tanai, 1955, 1961; Tanai & Suzuki, 1963).
9. Wakamatsu coal mine 2 km from Kanegasawa Bridge ca. 15 km south of Higashisetana Station near Wakamatsu (42°20'N, 139°56'E), Kudo coal-bearing member, Kunnui Formation, late early to early middle Miocene (Tanai, 1961; Tanai & Suzuki, 1963).
10. Abura flora near Setana (42°27'N, 139°52'E), Kunnui Formation, late early to early middle Miocene (Tanai, 1955, 1961; Tanai & Suzuki, 1963).
11. Soya-Magaribuchi, Hokutaku-koishi and Horonobe coal mines of the Tempoku coal field near Wakkanai (45°20'N, 142°20'E), Soya coal-bearing Formation, early Miocene (Endo, 1936, 1955; Tanai, 1955, 1961).
12. Cliff in the middle course of the Sakipempetsu River located about 20 km south of Ashibetsu (43°29'N, 142°14'E), Sorachi coal field, Ashibetsu District, Sakipempetsu flora, Sakipembersu/Nokonan Formation, Ishikari Group, early Miocene (Tanai, 1955, 1961, 1971).
13. Asahi coal mine, Ikushumbetsu District, Ishikari coal field near Yubari (43°04'N, 141°59'E), Asahi Formation, early Miocene (Tanai, 1955, 1961).
14. Honjin-no-sawa near Rumoi City (43°57'N, 141°40'E), Urye District, Rumoe coal field, Honjin-no-sawa Formation, late early to early middle Miocene (Tanai, 1955, 1961).
15. Hidaka coal area (ca. 42°50'N, 142°50'E), Niipaku Formation, late Miocene (Tanai, 1961).
16. Utanobori (ca. 44°50'N, 142°40'E), Kitami region, Tachikarabetsu Formation, late Miocene (Tanai, 1961).
17. Konomai mine (44°07'N, 143°30'E), Kitami Province, Shanabuchi Formation, late Miocene (Tanai, 1961).

11.11.2. Honshu

18. Aburato, Kozunohama, Sanze and Iragawa (Tagawa coal mine) near Oyama (38°40'N, 139°40'E), Nishitagawa coal field, Yamagata Prefecture, Atsumi, Aburato and Iragawa Formations, early early

Miocene (Tanai, 1952a, 1955, 1961; Huzioka, 1964; Matsue & Onoe, 1995).

19. Kamigo (38°15’N, 140°08’E) eastern and southern part of the Nishitagawa coal field, Yamagata Prefecture, Kamigo Formation, middle Miocene (Tanai, 1952b, 1961).
20. Oguni (38°03’N, 139°45’E), Yamagata Prefecture, Imaichi and Oguni Formations, middle Miocene (Morita, 1932; Tanai, 1955, 1961; Tokunaga, 1960; Onoe, 1974).
21. Along the Shira River near Yonezawa (ca. 38°00’N, 139°47’E), Okitama lignite field, Yonezawa Basin, Yamagata Prefecture, Takamine and Tenoko Formations, Shirakawa Group, late Miocene (Tokunaga & Tanai, 1954; Tanai, 1961; Uemura, 1988).
22. Shinjo Basin (38°43’N, 140°06’E), Yamagata Prefecture, Oriwata Formation, early Pliocene (Tanai, 1961).
23. Shichiku flora located ca. 8 km west of Yotsukura (36°50’N, 140°45’E), Joban coal field, Fukushima Prefecture, Shichiku Formation, early early Miocene (Tanai & Onoe, 1959; Tanai, 1961; Huzioka, 1964).
24. Koya (37°02’N, 140°49’E), Uchigo City, Fukushima Prefecture, Shichiku flora, Iwake Formation, Oligocene (Nathorst, 1888; Endo, 1963).
25. Shichuku flora near Iwaki City (ca. 37°00’N, 140°53’E), Fukushima Prefecture, Shirasaka Formation, Shiramizu Group, early to middle Miocene (Tanai & Onoe, 1959; Tanai, 1961).
26. Koyanaizu Village (37°31’09”N, 139°44’40”E), Yanaizu-machi, Kawanuma-gun, Aizu Basin, Fukushima Prefecture, Izumi Formation, Yamato Group, late Pliocene (Suzuki, 1961, 1987; Tanai, 1961; Manabe *et al.*, 1970).
27. River cliff along the Sakase River ca. 400 m S30°W of Matsuzuka Village (37°29’03”N, 139°46’53.6”E), Niitsura-mura, Oonuma-gun, Aizu Basin, Fukushima Prefecture, Izumi Formation, Yamato Group, late Pliocene (Suzuki, 1961, 1987; Tanai, 1961; Manabe *et al.*, 1970).
28. River cliff along the Wasedani River at Wasedani Village (37°41’15.7”N, 139°45’56.4”E), Yamato-machi, Yama-gun, Aizu Basin, Fukushima Prefecture, Izumi Formation, Yamato Group, late Pliocene (Suzuki, 1961, 1987; Tanai, 1961; Manabe *et al.*, 1970).
29. Hara River near Obusegawa Village (34°23’N, 135°18’E), Fukushima Prefecture, Nisihaga flora (Shiroko florule), Fujitoge Formation, late Miocene and Izumi Formation, late Pliocene (Suzuki, 1951, 1959; Tanai, 1961).
30. Tennoji (37°48’N, 140°25’E), Fukushima Prefecture, Tennoji flora, Tennoji Formation, late Miocene (Suzuki, 1959; Tanai, 1961).
31. Fukurohara (37°37’N, 139°43’E), Fukushima Prefecture, Fukurohara flora, Maki and Ootezawa floras, Izumi Formation, Yamato Group, Pleistocene (Suzuki, 1959).

32. Koyanaizu (37°31'N, 139°44'E), Fukushima Prefecture, Koyanaizu flora, Fuji-toge and Izumi Formations, Yamato Group, Plio-Pleistocene (Suzuki, 1959).
33. Shiotsubo (37°36'N, 139°45'E), Fukushima Prefecture, Shiotsubo flora, Shiotsubo Formation, Pliocene (Suzuki, 1959).
34. Higashidate (36°52'N, 140°26'E), Fukushima Prefecture, Higashidate flora, Kuroiwa Formation, Pliocene (Suzuki, 1959).
35. Kuji (40°12'N, 141°47'E), Iwate Prefecture, Sawayama Formation, Kuji Group, Senonian (Tanai, 1979).
36. River in Gamono, Mataki Village (38°50'N, 140°13'E), Nisiiwai District, Iwate Prefecture, Plio-Pleistocene (Miki, 1950b).
37. Sehara Cliff, Hiraizumi Village (38°59'N, 141°12'E), Nisiiwai District, Iwate Prefecture, Plio-Pleistocene (Miki, 1950b).
38. Morioka City (39°43'N, 141°08'E), Iwate Prefecture, Gosho flora, Masuzawa Formation, middle Miocene (Murai, 1957a, 1957b; Tanai, 1961).
39. Shin-Suzumeda colliery, Kaji colliery, Dan, Hirabara colliery, Okinoyama colliery, Wakayama colliery, Daini-Fuji colliery, Hagimori colliery, Shin-Suwa colliery, Fujimagari, Kami-Umeda, Motoyama colliery and Ejioike near Ube (33°57'N, 131°16'E), Yamaguchi Prefecture, Okinoyama Formation, Ube Group, late Eocene and possibly middle Eocene (Huzioka & Takahashi, 1970; K. Uemura personal communication, 2001).
40. Yamane, Yuya Village (34°21'N, 131°03E), Yuya Bay, Yamaguchi Prefecture, Hitomaru Formation, Hioki Group, early to middle Miocene (Huzioka, 1974).
41. Lignite bed in Azina (34°11'N, 131°57'E), Huzikawa Village, Kuma District, Yamaguchi Prefecture, Plio-Pleistocene (Miki, 1950b).
42. Ouchiyama-kami in Heki-cho about 14 km west of Nagato City (34°20'N, 131°13'E), Yamaguchi Prefecture, Kiwado Formation, Hioki Group, Oligocene (Uemura *et al.*, 1999).
43. Shiogama City and Saura-machi (38°20'N, 140°59'E) Miyagi District, Miyagi Prefecture, Sauramachi and Ajiri Formations, early and middle Miocene (Endo, 1931, 1933b, 1936, 1954; Tanai, 1955).
44. Near Sendai (38°16'N, 140°52'E), Miyagi Prefecture, Kameoka Formation, Sendai Group, early Pliocene (Endo, 1931, 1933a, 1933b; Tanai, 1961).
45. Akiho Village (ca, 38°15'N, 140°52'E) near Sendai, Miyagi Prefecture, Kameoka Formation, Sendai Group, early Pliocene (Kryshtofovich, 1920).
46. Sarao and Shizuhara near Fukui City (36°06'N, 136°13'E), Hokuriku District, Fukui Prefecture, Asuwa flora, Sarao bed, Paleocene (Matsuo, 1962).

47. Shimoichi and Fukaya (36°13’N, 136°10’E), Fukui, Fukui Prefecture, Kunimi Formation, middle Miocene (Huzioka, 1955; Tanai, 1961).
48. Monzen locality near Monzen (39°56’N, 139°47’E), Oga Peninsula, Akita Prefecture, Monzen Formation, early Miocene (Tanai, 1955; Huzioka, 1964).
49. Yakuya River, a tributary of the Yoneshiro River near Hanawa (ca. 40°15’N, 140°20’E), Akita Prefecture, Senosawa Formation, early Miocene (Huzioka, 1964).
50. Iwadate locality (formerly Hassei coal mine; 40°24’N, 139°43E), Hachimori-machi, Yamamoto District, Akita Prefecture, Iwadate coal-bearing Formation, early Miocene (Tanai, 1955, 1961; Huzioka, 1964).
51. Yokone florule near Honjo (39°23’N, 140°03’E) Akita Prefecture, Yokonetoge Formation, early Miocene (Huzioka, 1964).
52. Moriyoshi-machi (40°06’N, 140°20’E), Tsuyukuma (Arase coal mine), Kayakusa (Kinryuzan coal mine; 39°58’N, 140°24’E), Yunotai, Nekko (Ooani coal mine), Koya, Haginari, Shimo Hinokinai Village (39°44’N, 140°35’E) and Osawagawa localities near Aniai (39°58’N, 140°24’E), Akita Prefecture, Aniai Formation, early Miocene (Yokoyama, 1886; Nathorst, 1888; Kryshtofovich, 1920; Endo, 1963; Huzioka, 1964).
53. Yamakayakusa (39°57’N, 140°22’E), Hadachi, Uttonaizawa, Totorinai, Tachinomatazawa, Onimatazawa and Tsuchikumazawa localities are all situated about 5–40 km southeast of Aniai (40°00’N, 140°26’E), Akita Prefecture, Utto Formation, middle Miocene (Tanai, 1955, 1961; Huzioka, 1963).
54. Omagoshi locality (40°35’N, 139°56’E), Iwasaki Village, Nishi-Tsugaru District, Aomori Prefecture, Iwadate coal-bearing Formation, early Miocene (Huzioka, 1964).
55. Funauchi Mine located in the Nishimeya Mountains about 15 km southwest of Hirosaki (39°22’N, 140°03’E), Aomori Prefecture, Fujikura flora, Kuroishizawa Formation, early Miocene (Huzioka, 1964).
56. Coal mine on the eastern side of Mt. Gozu located about 15 km northeast of Gosen (37°47’N, 139°30’E), Sasaoka Village, Kita-Kambara District, Niigata Prefecture, Yamanokami Formation, early Miocene (Huzioka, 1964).
57. Zenshino, Terabora, Nishikatabira and Higashikatabira all located about 10 km southwest of Minokamo (35°29’N, 137°01’E), Aichi Prefecture, Nakamura Formation, Kani Group, early Miocene (Tanai, 1955; Huzioka, 1964; Ina, 1992).
58. Near Mizumani (35°25’N, 137°16’E), Aichi Prefecture, Toki Formation, Mizunami Group, Miocene (Tokunaga & Onoe, 1969).

59. Near Kouwa (34°44’N, 136°57’E), Chita Peninsula, Aichi Prefecture, Kouwa flora, Kouwa Member, Tokoname Formation, Seto Group, late Miocene (Miki, 1948; Ozaki, 1991).
60. Ueno, Sakashita-cho, Kasugai City (35°15’N, 136°57’E), Aichi Prefecture, Yadagawa Formation, late Miocene-early Pliocene (Miki, 1948, 1950b; Ozaki, 1991).
61. Syurakuen Cliff in Tita District (35°03’N, 135°55’E), Aichi Prefecture, early Pliocene (Miki 1941).
62. Fuchu City 15–20 km west of Tokyo (35°41’N, 139°30’E), Tokyo Prefecture, Minamitama Formation, (Miura Formation), middle Miocene (Ida, 1955).
63. Itoh mine, Obata-machi, Seto (35°08’N, 136°55’E), Aichi Prefecture, Seto porcelain clay Formation, late Miocene (Ozaki, 1991).
64. B bed in Bessyoyama, Hirakata City (34°50’N, 135°40’E), Osaka Prefecture, Plio-Pleistocene (Miki, 1950b; Uemura, personal communication 2003).
65. Itsukaichi (35°44’N, 139°13’E) in Akiruno City near Tokyo, Tokyo Prefecture, Kosho Formation, early Miocene (Endo, 1963; Uemura *et al.*, 2001).
66. Kita-asa River in Narahara, Hachioji City (35°40’N, 139°20’E), Tokyo Prefecture, Oyabe Formation, Plio-Pleistocene (Kimura *et al.*, 1981; Horiuchi, 1996).
67. Numerous localities near Kobe (ca. 34°40’N, 135°07’E), Hyogo Prefecture, Miocene (Hori 1987).
68. Asiyagawa Cliff (34°43’N, 135°18’E), Hyogo Prefecture, early Pliocene (Miki, 1941).
69. Toyooka (35°35’N, 134°48’E), Hyogo Prefecture, Toyooka and Akeyo Formations, Hokutan Group, Miocene (Tanai, 1961; Onoe, 1978).
70. *Stegodon* beds in Yagi near Akashi (34°38’N, 134°55’E), 25 km west of Kobe, Hyogo Prefecture, Pliocene (Miki, 1936, 1937, 1950a; Endo, 1954, 1955).
71. Nagurayama clay bed, Hayasida-ku (34°55’N, 134°35’E), Hyogo Prefecture, Plio-Pleistocene (Miki, 1950b; Uemura, personal communication 2003).
72. Zyoho Cliff (34°15’N, 134°45’E), Nada Village, Mihara District, Hyogo Prefecture, Plio-Pleistocene (Miki, 1950b).
73. Noboritate clay bed (34°15’N, 134°45’E), Tui-tyo, Mihara District, Hyogo Prefecture, Plio-Pleistocene (Miki, 1950b).
74. Lignite at Hukakusa (34°25’N, 134°52’E), Yamada Village, Tuna District, Hyogo Prefecture, Plio-Pleistocene (Miki , 1950b).

75. Lignite bed in Tamon, Nisimaiko, Akashi City (34°40'N, 135°00'E), Hyogo Prefecture, Plio-Pleistocene (Miki, 1950b; Uemura, personal communication 2003).
76. Kaminotani, Suma District, Kobe (34°41'N, 135°12'E), Hyogo Prefecture, Shirakawa Formation, Kobe Group, Oligocene (Shikama, 1938; Tanai, 1955, 1961).
77. Akashi (34°40'N, 134°58'E), Hyogo Prefecture, Akashi Formation, Osaka Group, early Pleistocene (Itihara, 1961).
78. Kobe (34°44'N, 135°22'E), Hyogo Prefecture, Akashi Formation, Osaka Group, early Pleistocene (Itihara, 1961).
79. Nishinomiya (34°39'N, 135°00'E), Hyogo Prefecture, Koyoen and Koroen members, Akashi Formation, Osaka Group, early Pleistocene (Itihara, 1961).
80. Rokko Highlands near Kobe (34°44'N, 135°22'E), Hyogo Prefecture, Kobe flora, Kobe Group, late Miocene (Hori, 1976, 1987).
81. Koyoen and Gokayama Cliffs and River cliff at Kantengoya, Nishinomiya City (34°45'N, 135°22'E), Hyogo Prefecture, Plio-Pleistocene (Miki, 1950b).
82. Nishiyagi, Okubo Village, Akashi District near Kobe (34°41'N, 134°52'E), Hyogo Prefecture, = Miki's (1937) *Stegodon* Beds, Osaka Group, Pliocene-early Pleistocene (Endo, 1936).
83. Kita-ku, Suma-ku and Nishi-ku (34°41'N, 135°06'E), Kobe, Hyogo Prefecture, Kobe Formation, Shirakawa Group, Oligocene (Kobayashi *et al.*, 1993).
84. Muraoka (35°24'N, 134°44'E), Youfu district, Hyogo Prefecture, Hokutan Formation, Takayanagi Group, middle Miocene (Kobayashi *et al.*, 1993).
85. Kasumi (35°39'N, 134°39'E), Shirosaki district, Hyogo Prefecture, Seto Volcanic Rock Formation, Miocene (Kobayashi *et al.*, 1993).
86. Muraoka (35°29'N, 134°34'E), Mikata distict, Hyogo Prefecture, Toyooka Group, Miocene (Ueji, 1938; Kobayashi *et al.*, 1993).
87. Hokudan-cho (34°31'N, 134°55'E), Tuna district, Hyogo Prefecture, Osaka Formation, Tomishima Group, Pliocene (Kobayashi *et al.*, 1993).
88. Miyamachi (34°27'N, 134°50'E), Tsuna district, Hyogo Prefecture, "lignite bed", Pliocene (Kobayashi *et al.*, 1993).
89. Seidan-cho (34°19'N, 134°43'E), Mihara district, Hyogo Prefecture, Pliocene (Kobayashi *et al.*, 1993).
90. Nandan-cho (34°14'N, 134°48'E), Mihara district, Hyogo Prefecture, Nada Formation, Pliocene (Kobayashi *et al.*, 1993).
91. Onsen-cho (35°29'N, 134°46'E), Mikata district, Hyogo Prefecture, Teragi Formation, late Miocene–Pliocene (Kobayashi *et al.*, 1993).
92. Shimotoda (34°59'N, 134°59E), Nishiwaki, Hyogo Prefecture, "*Metasequoia* bed", Plio-Pleistocene (Miki, 1950b; Kobayashi *et al.*, 1993).

93. Hagiwara (34°52'N, 135°24'E), Kawanishi, Hyogo Prefecture, "*Metasequoia* bed", Plio-Pleistocene (Kobayashi *et al.*, 1993).
94. Nonoike-chosuichi (34°41'N, 134°57'E), Akashi, Hyogo Prefecture, Kawanishi-clay, early Pleistocene (Kobayashi *et al.*, 1993).
95. Ookubo-cho (34°41'N, 134°57'E), Akashi, Hyogo Prefecture, lower Osaka Formation, early Pleistocene (Kobayashi *et al.*, 1993).
96. Nishi-ku (34°42'N, 135°06'E), Kobe, Hyogo Prefecture, lower Osaka Formation, Plio-Pleistocene (Kobayashi *et al.*, 1993).
97. Nagata-ku (34°41'N, 135°10'E), Kobe, Hyogo Prefecture, lower Osaka Formation, early Pleistocene (Kobayashi *et al.*, 1993).
98. Hibarigaoka (34°49'N, 135°26'E), Takarazuka, Hyogo Prefecture, "*Pinus koraiensis* bed" middle-late Pleistocene (Kobayashi *et al.*, 1993).
99. Gokayama, Shyurinji and Yama-Ashiyamachi (34°46'N, 135°20'E), Nishinomiya and Ashiya, Hyogo Prefecture, lower Osaka Formation, early Pleistocene (Kobayashi *et al.*, 1993).
100. Tarumi-ku, Kobe and Ohkuraya, Akashi (34°39'N, 135°03'E), Hyogo Prefecture, lower Osaka Formation, Plio-Pleistocene (Kobayashi *et al.*, 1993).
101. Kigo (35°33'N, 135°12'E), Kyoto Prefecture, Seya Formation, early early Miocene (Tokunaga & Onoe, 1969; Onoe, 1978).
102. Okukaizi clay bed (34°55'N, 135°43'E), Kaizi Village, Otokuni District, Kyoto Prefecture, Plio-Pleistocene (Miki, 1950b).
103. Fukakusa (34°56'N, 135°46'E), southeast of Kyoto, Kyoto Prefecture, Izumi Formation, Osaka Group, Pliocene (Fukakusa Research Group, 1962).
104. Miyazu City (35°33'N, 135°12'E), Kyoto Prefecture, Yosa Group, Seya Formation, early to middle Miocene (Tanai, 1961).
105. Yasaka (35°43'N, 135°02'E), Kyoto Prefecture, Seya Formation, early early Miocene (Onoe 1978).
106. Near Takaya and Orito (37°30'N, 137°15'E), Noto Peninsula, Ishikawa Prefecture, Yanagida Formation (= Higashi Innai Formation, Orito Member), early early Miocene (Ishida & Masuda, 1956; Tanai, 1961; Ishida, 1970).
107. Ningyo Pass (35°27'N, 133°52'E), Tottori Prefecture, Ningyo-Toge Formation, late Miocene (Tokunaga & Onoe, 1969).
108. Saji River located 200 m east-northeast of Tatsumi Pass (35°14'N, 134°07'E), Tottori Prefecture, Tochiwara Formation, late Miocene (Ozaki, 1979; Matsue & Onoe, 1995).
109. Fuganji, Takakubo and Dogo (34°13'N, 132°35'E), Tottori and Shimane Prefectures, Honshu, Suki and Fuganji Formations, Tottori Group, Miocene (Hojo, 1973).
110. Huke (34°19'N, 135°10'E) and Tsutimaru (34°22'N, 135°20'E) clay beds in Sennan District, Osaka Prefecture, early Pliocene (Miki, 1941).

111. Tannowa clay bed (34°20'N, 135°15'E), Sennan District, Osaka Prefecture, Plio-Pleistocene (Miki, 1950b).
112. Singe clay bed (34°20'N, 135°15'E), Higasitotori Village, Sennan District, Osaka Prefecture, Plio-Pleistocene (Miki, 1950b).
113. Clay bed in riverside (34°28'N, 135°42'E), Nisigori Village, Minamikawati District, Osaka Prefecture, Plio-Pleistocene (Miki, 1950b).
114. Hamuro clay bed (34°28'N, 135°42'E), Sinaga Village, Minamikawati District, Osaka Prefecture, Plio-Pleistocene (Miki, 1950b).
115. Kitahurue (34°57'N, 135°25'E), Hosokawa Village, Toyono District, Osaka Prefecture, Plio-Pleistocene (Miki, 1950b).
116. Lignite bed in Baba (34°53'N, 135°40'E), Kiyotani Village, Mishima District, Osaka Prefecture, Plio-Pleistocene (Miki, 1950b).
117. Near Kishiwada (34°27'N, 135°22'E), Osaka Prefecture, Sennan Formation, Osaka Group, late Pliocene, Kokubu Formation, Osaka Group, early Pleistocene (Momohara, 1992).
118. Suita-Ibaragi, Senriyama (34°48'N, 135°40'E), Osaka Prefecture, Senriyama Formation, Osaka Group, early Pleistocene (Itihara, 1961).
119. Hirakata-Sinkori, Hirakata near Osaka (34°48'N, 135°40'E), Osaka Prefecture, Senriyama Formation, Osaka Group, early Pleistocene (Itihara, 1961).
120. Izumisunagawa, Sennan near Osaka (34°29'N, 135°40'E), Osaka Prefecture, Senriyama Formation, Osaka Group, early Pleistocene (Itihara, 1961).
121. Lignite bed at Koda (34°12'N, 135°17'E), Arakawa Village, Naka District, Wakayama Prefecture, Plio-Pleistocene (Miki, 1950b).
122. Toge clay bed (34°20'N, 135°42'E), Hasimoto City, Ito District, Wakayama Prefecture, Plio-Pleistocene (Miki, 1950b; Oishi, 1950).
123. Kinokawa River, Hashimoto City (34°20'N, 135°36'E), Wakayama Prefecture, Shobudani Formation, Osaka Group, late Pliocene-early Pleistocene (Miki, 1941, 1950b; Momohara *et al.*, 1990).
124. Hashimoto clay (34°05'N, 135°15'E), Wakayama Prefecture, Plio-Pleistocene (Miki 1941, 1950b).
125. Sidatani clay bed (34°48'N, 136°10'E), Simagahara, Ayama District, Mie Prefecture, early Pliocene (Miki, 1941, 1950b).
126. Near Inabe-cho (35°10'N, 136°28'E), Inabe area, Mie Prefecture, Tokai Group, Kono and Ichinohara Formations, Pliocene, Oizumi Formation, late Pliocene-early Pleistocene and Komeno Formation, Pleistocene (Takemura, 1984).
127. Lignite bed in Sabutani (34°48'N, 136°10'E), Nii Village, Ayama District, Mie Prefecture, Plio-Pleistocene (Miki, 1950b).
128. Tarusaka clay bed, Ooyati Village (34°48'N, 136°10'E), Mie District, Mie Prefecture, Plio-Pleistocene (Miki, 1950b).

129. Yamanoisiki clay bed (35°03'N, 136°30'E), Mie Village, Mie District, Mie Prefecture, Plio-Pleistocene (Miki, 1950b).
130. Syukuno clay bed (35°03'N, 136°30'E), Komono-tyo, Mie District, Mie Prefecture, Plio-Pleistocene (Miki, 1950b).
131. Tyayagami clay bed (34°48'N, 136°10'E), Komono-tyo, Mie District, Mie Prefecture, Plio-Pleistocene (Miki, 1950b).
132. Lignite bed at Hagasikaino, Toyashiro Village (35°10'N, 136°28'E), Inabe District, Mie Prefecture, Plio-Pleistocene (Miki, 1950b).
133. Tadogawa clay bed (35°10'N, 136°33'E), Todo Village, Kuwana District. Mie Prefecture, Plio-Pleistocene (Miki, 1950b).
134. Kono clay bed (35°10'N, 136°33'E), Komi Village, Kuwana District, Mie Prefecture, Plio-Pleistocene (Miki, 1950b).
135. Hanataka lignite beds near Takasaki City (36°20'N, 139°06'E), Gunma Prefecture, early Pliocene (Miki, 1941, 1950).
136. Annaka City 9 km west of Takasaki (36°19'N, 138°55'E), Gunma Prefecture, Itahana Formation, late Miocene (Ozaki *et al.*, 1981; Ozaki, 1991; Horiuchi, 1996).
137. Yoshigayatsu Pass south of Annaka City (36°12'N, 138°50'E), Gunma Prefecture, Itahana and Akima Formations, late Miocene-early Pliocene (Horiuchi, 1996).
138. Akima near Annaka City (36°20'N, 139°00'E), Gunma Prefecture, Akima Formation, early Pliocene (Horiuchi, 1996).
139. Kaorizawa Valley, Katashina Village (ca. 36°47'N, 139°37'E), Tone District, Gunma Prefecture, Okunikko Rhyolites, Ohamami Formation, Maastrichtian (Kimura & Okawara, 1986).
140. Lignite bed in Okamidani (34°50'N, 133°50'E), Mayagami Village, Mitu District, Okayama Prefecture, Plio-Pleistocene (Miki, 1950b).
141. Lignite bed in Kosoku (34°30'N, 136°01'E), Nakayumon Village, Uda District, Nara Prefecture, Plio-Pleistocene (Miki, 1950b).
142. Lignite bed in Nishiada (34°28'N, 135°53'E), Ooada Village, Uda District, Nara Prefecture, Plio-Pleistocene (Miki, 1950b).
143. Ayamegaike Cliff (34°40'N, 135°40'E), Husimi Village, Ikoma District, Nara Prefecture, Plio-Pleistocene (Miki, 1950b).
144. Southeastern part of Nara City (35°53'N, 137°30'E), Nara Prefecture, Fujiwara Formation, Pliocene (Kokawa, 1954, 1955).
145. Numerous localities near Mt. Mikasa and Mt. Kasuga (34°41'N, 135°51'E), Nara Prefecture, Shirakawaike and Saho Formations, Plio-Pleistocene (Kokawa, 1954).
146. Nisinotanda clay bed (ca. 34°53'N, 136°12'E), Ohara Village, Koga District, Shiga Prefecture, Plio-Pleistocene (Miki, 1950b).
147. Somakawa clay bed (ca. 34°53'N, 136°12'E), Kibukawa-cho, Koga District, Shiga Prefecture, Plio-Pleistocene (Miki, 1950b).

148. Lignite bed in Nisidera (ca. 34°53’N, 136°12’E), Isebe-cho, Koga District, Shiga Prefecture, Plio-Pleistocene (Miki, 1950b).
149. Lignite bed in Hata (ca. 34°53’N, 136°12’E), Mikumo Village, Koga District, Shiga Prefecture, Plio-Pleistocene (Miki, 1950b).
150. Hara clay bed (35°02’N, 136°14’E), Higasisakuradani Village, Gamo District, Shiga Prefecture, Plio-Pleistocene (Miki, 1950b).
151. Lignite bed in Keikake Village (35°02N, 136°14’E), Gamo District, Shiga Prefecture, Plio-Pleistocene (Miki, 1941, 1950b).
152. Kozuhata clay bed (35°02’N, 136°14’E), Itihara Village, Gamo District, Shiga Prefecture, Plio-Pleistocene (Miki, 1950b).
153. Lignite bed in Shida, Taga Village (35°13’N, 136°17’), Inukami District, Shiga Prefecture, Plio-Pleistocene (Miki, 1950b).
154. Minamigaito and Fukuzawa located about 10 km north of Mizunami City (35°22’N, 137°15’E), Gifu Prefecture, Nakamura Formation, Kani Group, early Miocene (Tanai, 1955; Huzioka, 1964; Ina, 1992).
155. Ishibora, Kamitoge and Maki located about 5 km north of Akechi (35°19’N, 137°22’E), Gifu Prefecture, Nakamura Formation, Kani Group, early Miocene (Tanai, 1955; Huzioka, 1964; Ina, 1992).
156. Nakagumi, Ueno, Yabasama, Miyasaki, Fushima, Seta, Wagata, Hirakaido, Tani and Mikasa located within 10 km to the northeast, east and southeast of Minokamo (35°29’N, 137°01’E), Gifu Prefecture, Nakamura Formation, Kani Group, early Miocene (Tanai, 1955; Huzioka, 1964; Ina, 1992).
157. Lignite bed at Matuo (35°20’N, 136°29’E), Sekigahara, Gifu Prefecture, Plio-Pleistocene (Miki, 1950b).
158. Hagihara Cliff (35°17’N, 136°30’E), Makita Village, Yoro District, Gifu Prefecture, Plio-Pleistocene (Miki, 1950b).
159. River cliff in Simotara (35°17’N, 136°30’E), Tara Village, Yoro District, Gifu Prefecture, Plio-Pleistocene (Miki, 1950b).
160. Simoyama clay bed (35°17’N, 136°30’E), Toki Village, Yoro District, Gifu Prefecture, Plio-Pleistocene (Miki, 1950b).
161. Inkyoyama near the Tokishi Railway Station, Toki City (35°20’N, 137°11’E), Gifu Prefecture, Yamanouchi, Kujiri and Shukunohora facies, Akeyo Formation, Mizunami Group, early late Miocene (Ozaki, 1974; Ina, 1992).
162. Hachiya (35°30’N, 137°03’E), Minokamo District, Gifu Prefecture, Hachiya flora, Hachiya and Nakamura Formations, Kani Group, early Miocene (Tanai, 1955; Ina *et al.*, 1983, 1985; Ina, 1992).
163. Tarui-cho (35°21’N, 136°31’E), Fuwa District, Gifu Prefecture, Tokai Group, early Pleistocene (Tsukagoshi *et al.*, 1997).
164. Osusawa clay bed, Tokitutyo near Mt. Mikuni (35°15’N, 137°12’E), Toki District, Gifu Prefecture, early Pliocene (Miki, 1941, 1950a, 1950b).

165. Mizunami and Toki district (35°22'N, 137°15'E), Toki (35°22'N, 137°13'E) and Kani district (35°27'N, 137°11'E), Gifu Prefecture, Nakamura and Hiramaki Formations, Kani and Mizunami Groups, early to middle Miocene (Tanai, 1955, 1961; Ina, 1981, 1992).
166. Nakagumi locality near Minokamo (35°29'N, 137°01'E) and Fukazawa locality near Mizunami (35°25'N, 137°16'E), Gifu Prefecture, Toki Coal-bearing Formation, Mizunami Group, early early Miocene (Tanai, 1961; Ina, 1992).
167. Mizunami (35°20'N, 137°15'E), Gifu Prefecture, Akeyo Formation, Mizunami Group, early Miocene, 16–17 Ma (Ina, 1974, 1992).
168. Mizunami (35°20'N, 137°15'E), Oidawara Formation, Mizunami Group, middle Miocene, 14.5–15.5 Ma (Ina, 1974; 1992).
169. Sayado clay bed (36°33'N, 140°03'E), Masikotyo, Haga District, Tochigi Prefecture, Plio-Pleistocene (Miki, 1941, 1950b).
170. Lignite bed in Koike (37°50'N, 140°50'E), Kasimatyo, Soma District, Fukushima Prefecture, Plio-Pleistocene (Miki, 1941, 1950b).
171. Cliff in Kodakohara (37°30'N, 139°45'E), Kawanisi Village, Kanuma District, Fukushima Prefecture, Plio-Pleistocene (Miki, 1950b).
172. Tozawa (39°11'N, 140°10'E), Takano Village, Nishi-Shirakawa District, Fukushima Prefecture, undefined, probably late early to early middle Miocene (Endo, 1954, 1955).
173. Nagai (37°37'N, 139°48'E), Kawanisi Village, Kawanuma District, Fukushima Prefecture, Izumi Formation, Pliocene (Endo, 1936).
174. Ara River near Kumagaya (36°08'N, 139°22'E), Saitama Prefecture, Yagii Formation, late Miocene (Ozaki, 1991).
175. Iruma River at Sasai (35°49'N, 139°20'E), Iruma City, Saitama Prefecture, Bushi Clay Member, Plio-Pleistocene (Kimura *et al.*, 1981; Sasai Fossil Forest Research Group, 1984; Horiuchi, 1996).
176. Ogawa (36°03'N, 139°11'E), Saitama Prefecture, Kanisawa Formation, late early-early middle Miocene (Horiuchi, 1996).
177. Kawamoto Town (36°07'N, 139°16'E), Saitama Prefecture, Yagii Formation, late middle Miocene (Horiuchi, 1996).
178. Sayama Hills (35°45'N, 139°22'E), Saitama Prefecture, Yatsu clay, Sayama Formation, Miura Group, Mio-Pliocene (Saitama Research Group & Kanto Quaternary Research Group, 1970).
179. Near Saigo (36°12'N, 133°19'E), Oki Island, Shimane Prefecture, Suki Formation, Tottori Group, Miocene (Hojo, 1973).
180. Hamada City (34°52'30"N, 132°03'43"E), Shimane Prefecture, Fukui flora, Kokubu Volcanics, Kokubu Group, early to middle Miocene and Tsunozu Formation, late Pliocene (Imamura, 1957; Tanai, 1961).
181. Izumo City (35°23'N, 132°43'E), Shimane Prefecture, Takakubo shale member, Nabeyama Formation, late early Miocene (middle Miocene in Tanai, 1961).

182. Yatsuka (35°30'N, 133°04'E), Shimane Prefecture, Koura Formation, early Miocene (Matsue & Onoe, 1995).
183. Yunotsu (34°57'N, 132°15'E), Shimane Prefecture, Tonotsu Formation, Plio-Pleistocene (Sakanoue & Fujita, 1981).
184. Kitago (ca. 36°40'N, 137°50'E), northwest part of Nagano Prefecture, Kitago Formation, late Pliocene-early Pleistocene (Tomizawa, 1958).
185. Omori, Azano (35°20'N, 137°40'E), Chiyo, Kamome and Ohira near Iida City (35°35'N, 137°50'E), Anan-cho, Nagano Prefecture, Oshimojo Formation, Tomikusa Group, early Miocene (Yokoyama, 1886; Kryshtofovich, 1920; Endo, 1963; Ina, 1988; 1992).
186. Kita-Aiki Village (36°02'N, 138°35'E) 10 km northeast of Yatsugadake, Minami-saku, Nagano Prefecture, Kita-Aiki Formation, Miocene (Nathorst, 1888; Kryshtofovich, 1920, 1930; Endo, 1963).
187. Ozamita and Muroga (ca. 36°25'N, 138°27'E), Chiisagata, Nagano Prefecture, undefined, probably Mio-Pliocene (Kryshtofovich, 1930).
188. Ussawa near Iida City (35°35'N, 137°50'E), Ysasuoka Village, Nagano Prefecture, Awano Formation, Tomikusa Group, early Miocene (Ina, 1988, 1992).
189. Chigisawa River near Iida City (35°35'N, 137°50'E), Anan-cho, Shimoina District, Nagano Prefecture, Nukuta Formation, Tomikusa Group, early Miocene (Ina, 1988, 1992).
190. Ogawa (35°53'N, 138°33'E), Nagano Prefecture, Sashikiri Member, Omi (Ogawa) Formation, middle Miocene (Kryshtofovich, 1930; Kon'no, 1931; Tanai, 1961; Ozaki, 1991).
191. Chausu-yama (35°22'N, 137°08'E), Shinonoi-machi, Nagano Prefecture, probably equivalent to Omi (Ogawa) Formation, middle Miocene (Tanai, 1961).
192. Kamikanezawa, Daigo Town approximately 30 km north of Omiya (36°46'N, 140°17'E), Ibaraki Prefecture, Asakawa and Kitatake Formations, late early to early middle Miocene (Nathorst, 1888; Oyama, 1960; Tanai, 1961; Endo, 1963; Horiuchi, 1996).
193. Hitachi-omiya (36°33'N, 140°24'E), Ibaraki Prefecture, Sakuramoto Formation, late early Miocene (Akutsu, 1952; Huzioka & Uemura, 1979; Horiuchi, 1996).
194. Inube Pass (36°37'N, 140°25'E), Yamagata Town, Ibaraki Prefecture, Asakawa Formation, late early to early middle Miocene (Horiuchi & Takimoto, 2001).
195. Kanasogo Town, Osato area 20 km north of Mito City (36°22'N, 140°29'E), Ibaraki Prefecture, Kume Formation, early Pliocene (Takimoto *et al.*, 1998).

11.11.3. Shikoku

196. Imoo clay bed (34°08’N, 133°45’E). Kamisaita, Saita Village, Kagawa Prefecture, Plio-Pleistocene (Miki, 1950b).
197. Sinme Cliff (34°12’N, 133°40’E), Sogo Village, Nakatado District, Kagawa Prefecture, Plio-Pleistocene (Miki, 1950b).
198. Lignite bed in Teradani (34°00’N, 134°15’E), Sanzi, Moriyama Village, Oe District, Tokushima Prefecture, Plio-Pleistocene (Miki, 1941, 1950b).
199. Numerous localities on Awaji Island (34°11’25”-34°32’48”N, 134°44’01”-134°59’05”E), Yudani, Atago and Goshikihama Formations, Osaka Group, late Pliocene (Momohara & Mizuno 1999).
200. Mizuwakare in the eastern part of Uwajima City (33°03’N, 132°43E), Ehime Prefecture, Takanoko Formation, late Pliocene-early Pleistocene (Mizuno, 1980).
201. Niihama City, Iyo-gun, Ehime Prefecture, undefined (Yagi, 1955).

11.11.4. Kyushu

202. Minami-Arima-cho (32°38N, 130°16’E; syn: Oe), Shimabara Peninsula, Minami-Arima-Village, Minami-Takaki District, Nagasaki Prefecture, Kuchinotsu Group, early Pleistocene (Endo, 1936; Takahashi, 1954).
203. Mogi near Nagasaki (32°42’N, 129°55’E), Nagasaki Prefecture, Mogi plant-bearing Formation, late Pliocene (Nathorst, 1883; Florin, 1920; Tanai, 1961, 1976; Endo, 1963).
204. Kazusa (ca. 32°50’N, 130°00’E), Shimabara, Nagasaki Prefecture, Sasebo Group, Oya Formation, Pliocene (Takahashi, 1954; Matsue & Onoe, 1995).
205. Oshima Colliery, Sasebo City (33°29’N, 129°32’E), Oshima Island, Nagasaki Prefecture, Sakito Formation, Matsushima Group, early Oligocene (Tanai, 1952a; Matsuo, 1970).
206. Kuchinotsu (32°28’N, 130°10’E), Nagasaki Prefecture, Oya and Kitaarima Formations, Kuchinotsu Group, early Pleistocene (Otsuka, 1966).
207. Lignite bed in Yunoso, Kodaragi Village, Kurume City (33°15’N, 130°31’E), Mizuma District, Fukuoka Prefecture, Pliocene (Miki, 1950b; Miki & Kokawa, 1962).
208. Lignite bed in Uchikoshi west of Kuroki Station (33°14’N, 130°39’E), Kitakawachi Village, Yame District, Fukuoka Prefecture, Pliocene (Miki, 1950b; Miki & Kokawa, 1962).
209. Near Nagano and Lake Imuta (31°47’N, 130°28’E; syn: Hiwaki), Kagoshima Prefecture, Nagano flora, Nagano, Koriyama and Tabira

Formations, late Pliocene (Onoe, 1972; Takayama & Hayasaka, 1975; Matsue & Onoe, 1995).

210. Iriki-cho near Yoshida Village (31°36’N, 131°00’E), Kagoshima Prefecture, Yamanokuchi Formation, early Pleistocene (Hase & Hatakana, 1976).
211. Locality about 10 km southwest of Sendai (31°50’N, 130°17’E) and another locality situated about 15 km south of Okuchi (31°43’N, 129°02’E), Kagoshima Prefecture, Daiwa Member, Koriyama Formation and Nagano Formation, late Pliocene (Hase & Hatanaka, 1984).
212. Koriyama Village, Gamou-cho and Hiwaki Village (ca. 31°48’N, 130°25’E), Satsuma Village (ca. 31°55’N, 130°27’E) and Kaseda City (31°20’N, 130°20’E), Kagoshima Prefecture, Kajiki, Gamou and Hayato Formations, Kokubu Group, early Pleistocene (Takaki, 1985, 1986).
213. Yunohara and Shitabarai (32°20’N, 130°45’E), Hitoyoshi City, Kumamoto Prefecture, Hitoyoshi Formation, Pliocene (Miki & Kokawa, 1962).
214. Hoshiwara, Kahoku-cho (33°10’N, 130°45’E), Kumamoto Prefecture, Hoshiwara flora Hoshiwara Member, Tsue Group, Pliocene (Iwao, 1981; Iwao & Matsuo, 1982).
215. Kujyu Village (33°13’N, 131°12’E), Ohita Prefecture, Nogami flora, Hosenji Member, Kusu Formation, Pleistocene (Endo, 1963; Iwao, 1981).
216. Kida, Shinminato, Hino and Nittetsu-Emukae coal mines of the Sasebo coal field near Sasebo (33°10’N, 129°42’E), Nagasaki Prefecture, Ainoura, Yunoki and Fukui Formations, Sasebo Group, early Miocene (Tanai & Onoe, 1956; Tanai, 1961).
217. Higashimatsuura Peninsula (33°32’N, 129°52’E), Saga Prefecture, Hachinokubo gravel bed, Miocene (Matsue & Onoe, 1995).

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Chapter 2

Paleoecology and History of *Metasequoia* in Japan, with Reference to its Extinction and Survival in East Asia

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Abstract: The occurrence of fossil *Metasequoia* Miki in and around Japan was reviewed based on recent stratigraphic and paleoenvironmental data to reconstruct the regional ecology and discuss the processes that led to the extinction of *Metasequoia* in Japan during the late Miocene and its survival in eastern Asia. The frequent and abundant occurrence of *Metasequoia* fossils with wetland plants during the Eocene indicates that *Metasequoia* was one of the dominant components of the flood plain wetland forests of Japan. In the Paleogene, *Metasequoia* was widely distributed in the vegetation zones located between the Paratropical Rain Forest and polar Mixed Coniferous Forest zones. *Metasequoia* populations in East Asia were limited by a mild maritime climate and were absent from the subtropical regions where fossil assemblages were represented by semi-arid sclerophyllous forests. Climatic cooling may have exterminated *Metasequoia* populations in northeastern China and the Russian Far East during the late Miocene. However, *Metasequoia* survived up until the latest early Pleistocene in central and southwestern Japan. *Metasequoia* was less common in the small subsiding basins than in the wide sedimentary

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basins that were associated with contiguous fluvial flood plain ecosystems. Thus, orogenic and volcanic induced changes in topography in the flood plains were also assumed to have influenced the distribution of *Metasequoia* since the late Miocene. These topographic changes culminated during the late early Pleistocene and were accompanied with eustatic events and likely exterminated *Metasequoia* populations in the alluvial lowlands in southwestern Japan and hindered the post-glacial migration of the genus.

Key words: early Pleistocene; East Asia; historical biogeography; local extinction; *Metasequoia*; paleovegetation; plant macrofossil; Tertiary; wetland forest.

1. INTRODUCTION

The genus *Metasequoia* Miki was described by Miki (1941) based on fossils collected from the Japanese Neogene prior to the discovery of the living plant. In the figures provided with the diagnosis and description, Miki illustrated a number of specimens that were obtained from four localities including two from the late Miocene and two from the Pliocene (Table 2-1), but he did not specify a holotype. Miki (1941) illustrated and described many isolated parts of the plant such as the shoots, leaves, cuticle, seeds and cones in an effort to reconstruct the whole plant and its paleoecology. In particular, he noted that the short shoots were deciduous. In addition to forming a new combination from *Sequoia disticha* Heer, *Metasequoia japonica* (Endo) Miki was also described as a new species having cones with a fewer number of cone scales than those of *M. disticha* (Heer) Miki (Miki, 1941), although both species are now considered to belong to a single fossil species, *M. occidentalis* (Newberry) Chaney (Liu *et al.*, 1999).

Table 2-1. Type localities of *Metasequoia* Miki (1941)

Localities	Location	Elevation (m)	Formation	Age (Ma)	Illustrations of Type Specimens
Osusawa, Tokitsu, Gifu Prefecture	30°20’ N, 137 °11’ E	160	Tokiguchi Porcelain Clay Formation	10	*M. disticha* (c, s, l, t) *M. japonica* (c)
Sidatani, Shimagahara, Mie Prefecture	34°44’ N, 136°03’ E	200	Ueno Formation	3.5	*M. disticha* (c, s)
Hanataka, Takasaki, Gunma Prefecture	36°20’ N, 138°57’ E	60	Lower Itahana Formation	8	*M. disticha* (t)
Toge, Hashimoto, Wakayama Prefecture	34°20’ N, 135°40’ E	120	Lower Shobudani Formation	1.7	*M. disticha* (t)

Legend: c = cone; t = twig; s = seed; l = leaves.

Miki's palaeobotanical studies were aimed to clarify the origin of the modern Japanese flora. As a result of his intensive studies on plant macrofossil assemblages from the Pliocene, Pleistocene and Holocene in and around the Kinki District, Central Japan, he classified the fossil assemblages into six "floral beds" including the Pliocene "*Metasequoia*" bed based on floral components and their stratigraphic position (Miki, 1948). The *Metasequoia* bed floral assemblage was characterized by the common occurrence of *Metasequoia* and other taxa that are now extinct from Japan including *Glyptostrobus* Endlicher, *Pseudolarix* Gordon, *Sequoia* Endlicher, *Cyclocarya* Iljinskaya and *Liquidambar* L. Since the 1950s, the stratigraphic positions of the fossil assemblages described by Miki (1948) have been re-examined in detail based on tephrochlonology and magnetostratigraphy and the "*Metasequoia* bed" floras have been assigned to the Pliocene and the early Pleistocene. Itihara (1961) determined that the horizon of the last occurrence of *Metasequoia* occurs in the Ma2 Marine Clay bed of the Osaka Group that was deposited during the latest early Pleistocene in the hills around Osaka Bay.

Floral change from the late Miocene to the Pleistocene in Japan is characterized by the extinction of plants that flourished during the Tertiary and an increase and/or emergence of elements that are dominant in the Recent cool-temperate and sub-alpine forests of Japan. The plants that are now extinct in Japan were most abundant in the earliest late Miocene floras from the Seto Porcelain Clay Formation and the correlative strata in Central Japan that Miki (1941) described as the "*Pinus trifolia* bed". This flora is rich in taxa that are endemic to the extant floras of the Yangtze River Valley in China.

The development of a monsoonal climate together with climatic deterioration occurred in eastern Asia during the late Miocene and the subsequent isolation of the Japanese Islands from the Asian continent during the late Pliocene. These events appear to have accelerated the development and differentiation of the modern and compositionally distinct Japanese floras from the ancient Miocene floras that show affinity with the modern Chinese floras seen in the Yangtze River Valley. Among the taxa that are now extinct in Japan, *Metasequoia* was a common constituent of the Japanese Neogene and survived in Japan up until the latest early Pleistocene. Prior to its extirpation, the latest early Pleistocene populations in Japan are the last known occurrence of the genus in the Northern Hemisphere. The survival and extinction of *Metasequoia* is an attractive subject to outline the development of the extant Japanese flora and vegetation. In this chapter, the occurrence of fossil *Metasequoia* in and around Japan is reviewed based on recent stratigraphic and paleoenvironmental data that have been used to reconstruct the regional ecology and past vegetation. The process that led to the extinction of *Metasequoia* since the late Miocene and its survival in eastern Asia are discussed.

2. OCCURRENCE AND PALEOECOLOGY OF *METASEQUOIA* IN THE LATE CRETACEOUS AND PALEOGENE FLORAS IN AND AROUND JAPAN

Records of *Metasequoia* fossils in Japan range from the Late Cretaceous to the early Pleistocene (LePage *et al.*, this volume). However, sediments including plant macrofossils deposited and preserved prior to the early Eocene are poor in Japan and the biogeography and ecology of *Metasequoia* are less certain during pre-Eocene time than in post-Eocene time. An example of a Late Cretaceous occurrence was reported from the Asuwa Formation in Fukui Prefecture, Central Japan. The fossil flora includes abundant *Metasequoia* shoots (11% of total 820 specimens), together with ferns, *Nilsonia* Brongniart, *Ginkgo* L., *Sequoia*, *Taxodium* Richard, Nymphaeaceae and other angiosperm leaves (Matsuo, 1962).

Metasequoia is a common constituent of the fossil assemblages that were deposited during the middle Eocene in Japan. Floral assemblages that are rich in tropical and subtropical taxa, including *Sabalites* Saporta and evergreen representatives of the Fagaceae, Lauraceae, Myrsinaceae and Sterculiaceae, characterize the middle Eocene floras in Japan. A fossil flora from the Ube Coalfield, in southwestern Japan (Locality 1, Figure 2-1), indicates the presence of a Paratropical Rain Forest (Wolfe, 1979) in southwestern Japan during the middle Eocene (Figure 2-1; Tanai, 1992). *Metasequoia* was the most common fossil element in the flora, and was represented in 13 of 27 localities with *Sabal chinensis* (Endo) Huzioka *et* Takahashi occurring as the second most commonly encountered plant (Huzioka & Takahashi, 1970). *Metasequoia* also occurs frequently in the middle Eocene localities in Hokkaido where a predominance of deciduous broad-leaved trees indicates that Notophyllous Broad-leaved Evergreen Forests dominated the region (Figure 2-1; Tanai, 1992). In the middle Eocene Yubari Formation from central Hokkaido (Locality 2, Figure 2-1), *Metasequoia* occurred frequently (12 of 18 localities) with other wetland plants such as *Equisetum arcticum* Heer, *Glyptostrobus europaeus* (Brongniart) Heer, *Planera ezoana* Oishi *et* Huzioka and *Cercidiphyllum arcticum* Brown (Huzioka & Kobayashi, 1961).

In the fossil assemblages that were deposited during the late Eocene and early Oligocene, both in Hokkaido and western Japan, representatives of the deciduous Salicaceae, Juglandaceae, Betulaceae, Ulmaceae, Platanaceae and Fagaceae became dominant and the number and geographic extent of the tropical-subtropical and evergreen broad-leaved trees decreased from the Paleogene to the Neogene (Tanai, 1992). *Metasequoia* however, continued to be a common constituent of the fossil assemblages. Numerical representation of

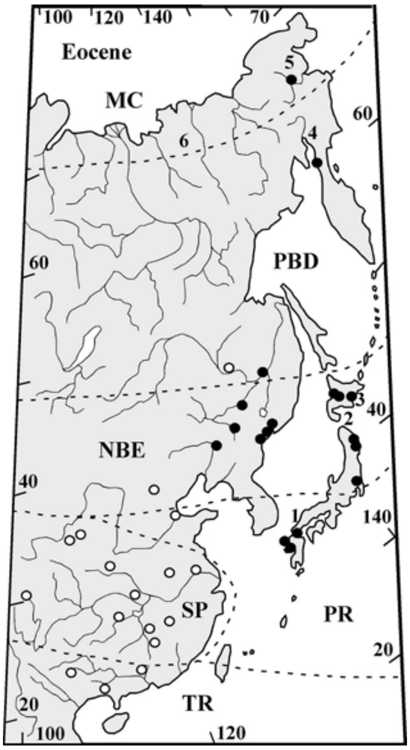

Figure 2-1. Distribution of *Metasequoia* fossils in the middle Eocene vegetation zones in Japan and eastern Asia. The vegetation zones are based on those defined by Tanai (1992). MC: Mixed Coniferous Forest; PBD: Polar Broad-leaved Evergreen Forest; NBE: Notophyllous Broad-leaved Evergreen Forest; PR: Paratropical Rain Forest; SP: Semi-arid Paratropical Forest and TR: Tropical Rain Forest. The ages of the fossil localities are based on Biske (1975), Fotyanova (1988), Varnavskii *et al.* (1988), Tanai (1992), Liu *et al.*, (1996), Budantsev (1997) & Leonov *et al.* (1999). Closed circle (●) = fossil localities where *Metasequoia* is present; open circle (○) = fossil localities where *Metasequoia* is absent. The localities are as follows: 1. Ube Coalfield (Huzioka & Takahashi, 1970); 2. Yubari (Huzioka & Kobayashi, 1961); 3. Kushiro (Tanai, 1970); 4. Chemurnaut (Budantsev, 1983); 5. Raritkin (Krishtofovich, 1958) and 6. Dzholoon-Sise (Biske, 1975).

fossil leaf floras described from the late Eocene Harutori Formation of the Kushiro Coalfield, Hokkaido (Locality 3, Figure 2-1; Tanai, 1970), and the Shirakawa and Aina Formations of the Kobe Group, western Japan (Locality 1, Figure 2-2; Hori, 1976), were correlated with the uppermost Eocene and lowermost Oligocene based on potassium-argon ages (31–36 Ma) obtained from volcanic ash (Ozaki, 1992). In the fossil assemblage of the Harutori Formation, *Metasequoia* shoots and cones accounted for 45.2 percent of a total of 6299 specimens. Among the 58 species of fossil plants identified from this

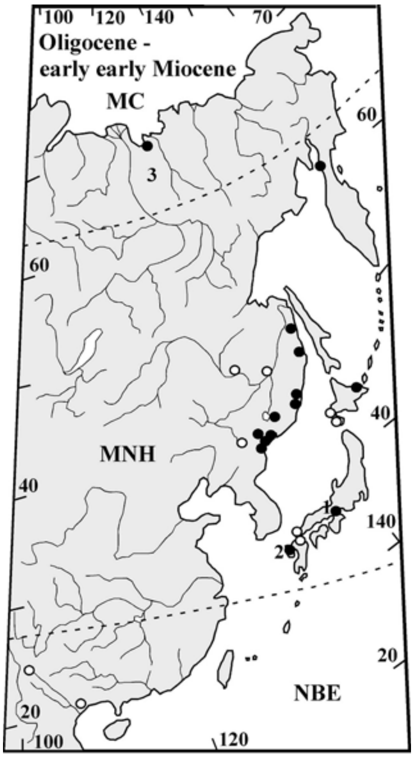

Figure 2-2. Distribution of *Metasequoia* fossils in the Oligocene to early early Miocene vegetation zones in Japan and eastern Asia. The vegetation zones are based on those defined by Tanai (1992). MC: Mixed Coniferous Forest; NBE: Notophyllous Broad-leaved Evergreen Forest and MNH: Mixed Northern Hardwood Forest. The ages of the fossil localities are based on Biske (1975), Fotyanova (1988), Varnavskii *et al.* (1988), Tanai (1992), Liu *et al.* (1996), Budantsev (1997) & Leonov *et al.* (1999). Closed circle (•) = fossil localities where *Metasequoia* is present; open circle (○) = fossil localities where *Metasequoia* is absent. The localities are as follow: 1. Kobe (Hori, 1976); 2. Sasebo (Tanai & Onoe, 1956); and 3. Sereha (Dorofeev, 1972).

assemblage, *Alnus hokkaidoensis* Tanai (9.2%), *Cercidiphyllum eojaponicum* Endo (4.1%), *Musophyllum nipponicum* Tanai (3.5%), *Cocculus ezoensis* Tanai (3.1%) and *Planera ezoana* (2.8%) were the most frequently encountered fossil plants. In the fossil assemblages of the Kobe Group, *Zelkova ungeri* (Ettingshausen) Kovats (5.8%), *Equisetum arcticum* Heer (4.9%), *Sequoia affinis* Lesquereux (4.6%), *Metasequoia occidentalis* (4.5%) and *Fagus cf. stuxbergii* (Nathorst) Tanai (4.1%) were the most commonly encountered plants in the 3941 specimens (57 species) collected from the assemblage. *Metasequoia* amounted for up to 49% of the fossils collected from one assemblage.

The middle and late Oligocene floras of Japan indicate that the composition of the Mixed Northern Hardwood Forests were dominated by deciduous broad-leaved trees and conifers with fewer evergreen broad-leaved trees (Figure 2-2). In the late Oligocene Ainoura flora of the Sasebo Coalfield, southwest Japan (Locality 2, Figure 2-2), evergreen broad-leaved trees were not identified and *Metasequoia* was represented at 7 of 9 localities, with the other common taxa including *Glyptostrobus* and *Plafkeria basiobliqua* (Oishi *et* Huzioka) Tanai of the Tiliaceae (Tanai & Onoe, 1956).

The frequent and abundant occurrence of *Metasequoia* in the Paleogene fossil assemblages in Japan together with other wetland taxa such as *Equisetum* L., *Glyptostrobus*, *Alnus* Miller and *Planera* Gmelin indicates that *Metasequoia* was one of the dominant components of the flood plain, wetland forests of Japan, which were situated at the margin of the Asian continent. The phytogeography of *Metasequoia* in and around Japan can be tracked by changes in the vegetation zones in eastern Asia since middle Eocene time (Figure 2-1; Tanai, 1992). In the middle Eocene, Paratropical Rain Forests and Notophyllous Broad-leaved Forests covered Japan, Polar Broad-leaved Deciduous Forests dominated in northern Sakhalin, and Mixed Coniferous Forests were distributed in the polar regions. Occurrences of *Metasequoia* in the middle Eocene Dzholoon-Sise locality in the lower reaches of the Omoloi River (Locality 5, Figure 2-1; Biske, 1975) and the Eocene Rarytkin locality in the lower reaches of the Anadyr River (Locality 6, Figure 2-1; Krishtofovich, 1958) show that *Metasequoia* was widely distributed between the northern part of the Paratropical Rain Forest and Polar Mixed Coniferous Forest zones. In addition, *Metasequoia* was absent from the mid-latitude Eocene localities in China (Liu *et al.*, 1996) where Semi-arid Paratropical Forests growing in an arid subtropical climate were composed largely of sclerophyllous trees (Tanai, 1992). Climatic deterioration at the Terminal Eocene Event changed the forest vegetation between southwestern Japan and northern Kamchatka to a Mixed Northern Hardwood Forest (Tanai, 1992). The occurrence of *Metasequoia* in the late Oligocene Sereha seed flora (Locality 3, Figure 2-2; Dorofeev, 1972) in the lower reaches of the Omoloi River indicates that *Metasequoia* still remained as a constituent of the Polar Mixed Coniferous Forest zone and did not change its distribution in eastern Asia during the Oligocene. Oligocene fossil sites are scarce in China and the distribution of *Metasequoia* in the continental mid-latitude regions of eastern Asia has not been fully elucidated.

3. GEOGRAPHICAL CHANGES IN THE DISTRIBUTION OF *METASEQUOIA* DURING THE NEOGENE AND EARLY PLEISTOCENE

Metasequoia is a common constituent of the early Miocene deposits of Japan. Early early Miocene (24–20 Ma) floras in Japan are characterized by deciduous broad-leaved trees with conifers (Huzioka, 1964; Tanai, 1961). The taxonomic diversity of the early Miocene floras, represented by the number of taxa in each flora, decreased as the number of thermophilous plants disappeared as climate cooled during the Oligocene (Tanai, 1992). However, *Metasequoia* continued to be well-represented together with *Picea* A. Dietrich, *Glyptostrobus*, *Alnus*, *Betula* L., *Carpinus* L., *Fagus antipofi* Heer and *Acer* L. at a number of fossil localities in Honshu (Huzioka, 1964), though it was absent at some localities in Hokkaido (Tanai & Suzuki, 1963, 1972).

The late early Miocene floras, are temporally distributed between 19 and 16 Ma, and characterized by high species diversity with an abundance of evergreen broad-leaved trees and subtropical elements that are part of the Notophyllous Broad-leaved Evergreen Forests that expanded to the north (Figure 2-3, Table 2-2). The percent of evergreen broad-leaved fossils in each flora increases from 7 to 27% in the more southern floras of Honshu, with an increase in the number of evergreen taxa including Fagaceae, Lauraceae and Theaceae. Evergreen broad-leaved trees were scarce and deciduous broad-leaved trees like *Fagus antipofi, Castanea* Miller*, Zelkova* Spach and *Acer* dominated the Mixed Northern Hardwood Forests of Hokkaido together with *Picea*. *Metasequoia* was common and abundant both in Honshu and Hokkaido at this time (Figure 2-3; Table 2-2).

Records of *Metasequoia* from the middle and upper Miocene floras in Japan decrease in contrast to that seen prior to the early Miocene. Fossil assemblages of the cool phase (14-10.5 Ma) following the earliest middle Miocene climatic optimum are scarce in Honshu and records of *Metasequoia* are unknown. The occurrence of *Metasequoia* in northeastern Hokkaido is limited to the Tachikaraushinai and Penkenai Formations (Locality 1, Figure 2-4; Tanai *et al.*, 1981), which are considered to have been deposited at about 13-14 Ma based on a Potassium-Argon age of the contemporaneous volcanic rocks (Shibata & Tanai, 1982). Those records represent the uppermost horizon of the occurrence of *Metasequoia* in Hokkaido.

The late Miocene distribution of *Metasequoia* in Japan was limited to localities in Honshu and becomes less frequent compared with that seen during the Paleogene and early Miocene (Figure 2-4; Table 2-3). Late Miocene floras are characterized by the dominance of deciduous broad-leaved trees and conifers (Table 2-3). *Salix* L., *Populus* and *Alnus* became frequent constituents of the floodplain vegetation as well as other deciduous broad-leaved trees like *Ulmus* L., *Betula*, *Carpinus*, *Quercus* L. and *Acer*. The most dominant species in Hokkaido was *Fagus palaeojaponica* Tanai *et* Onoe, while in Honshu *F. stuxbergii* was dominant. The relative abundance of beech in fossil assemblages sometimes exceeded 50% of the total number of species encountered in fossil assemblages both in Hokkaido and Honshu. The presence of evergreen broad-leaved elements together with deciduous subtropical elements indicates

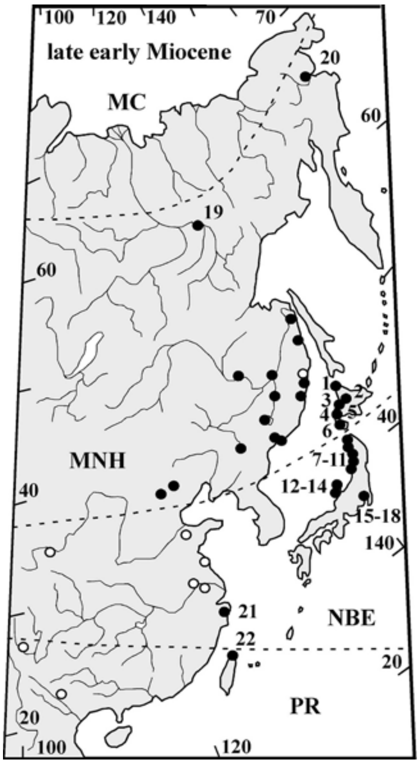

Figure 2-3. The distribution of *Metasequoia* fossils in the late early Miocene vegetation zones of Japan and eastern Asia. Abbreviations of the vegetation zones (Tanai, 1992) are MC: Mixed Coniferous Forest; MNH: Mixed Northern Hardwood Forest; NBE: Notophyllous Broad-leaved Evergreen Forest and PR: Paratropical Rain Forest. Closed circle (•) = *Metasequoia* is present and an open circle (○) = *Metasequoia* is absent. The ages of the fossil localities are based on Huzioka (1972), Biske (1975), Fotyanova (1988), Varnavskii *et al.* (1988), Tanai (1992) and Liu *et al.* (1996). Locality data other than 19 (Mammoth Mountain—Dorofeev, 1969), 20 (lower horizons of North-Pekul'neyveem—Nikitin, 1979), 21 and 22 (Ninghai and Shihting, respectively—Liu *et al.*, 1996) are based on Momohara (1997) (Tables 2-2 and 2-3). Localities include the following: 1. Soya; 2. Takinoue; 3. Abura; 4. Wakamatsu; 5. Kudo; 6. Yoshioka; 7. Fujikura; 8. Utto; 9. Kamigo; 10. Osudo; 11. Oguni; 12. Noroshi; 13. Notonakajima; 14. Tatsunokuchi; 15. Tomikusa; 16. Agi; 17. Toyama; and 18. Hiramaki.

that the Mixed Mesophytic Forests were distributed in and around central Japan, while the fossil floras from northeastern and western Honshu indicate that these regions were dominated by Mixed Northern Hardwood Forests. *Metasequoia* is often found in fossil assemblages from northern and central Honshu at this time, but it is less frequent than that seen during the middle Miocene. For example, *Metasequoia* was found from only one locality among the 13 described by Miki (1941) in the late Miocene Seto Porcelain Clay Formation and its

Table 2-2. Occurrence of selected fossil plants from the late early to earliest middle Miocene of Japan (18–15 Ma) (after Momohara, 1997)

Fossil taxa	Extant relatives	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Cercidiphyllum crenatum (Unger) Brown	*C. japonicum* Siebold *et* Zuccarini	+		+		+	+												
Fagus antipofi Heer				●	⊙	●			+	+		+					+		
Picea ugoana Huzioka	*P. bicolor Mayr*			○	+	⊙	+					+							
Alnus protomaximowiczii Tanai	*A. maximowiczii* Callier			+	○	⊙	○		○										
Acer rotundatum Huzioka	*A. mono* Maximowicz			○	○	⊙	○		○	+		+	+						
Glyptostrobus europaeus (Brongniart) Heer	*G. pensilis* Koch	⊙	*	○		+	+	*	⊙		○		+	+					
Acer ezoanum Oishi *et* Huzioka	*A. miyabei* Maximowicz	+		○	○	●	⊙			+			+			○	⊙	+	
Castanea miomollissima Hu *et* Chaney	*C. mollissima* Blume			○	●		●		⊙	⊙	○	⊙	○	○	○	⊙	○	○	○
Zelkova ungeri (Ettingshausen) Kovats	*Z. serrata* (Thunb.) Makino		*	+	●	⊙	●	*	⊙	⊙	●	●	●	○	⊙	⊙	⊙	⊙	⊙
Metasequoia occidentalis (Newberry) Chaney	*M. glyptostroboides* Hu *et* Cheng	⊙	*	⊙	○		○		⊙	+	+	+	○	+	+	⊙	○	○	○
Pterocarya Kunth spp.		+	*		+	+	+	*	⊙	○	○	○	○			●	○	○	⊙
Comptonia naumanni (Nathorst) Huzioka	*C. peregrina* (L.) Coulter		*	+	+	●	+	*	⊙	⊙	+	●	⊙	○	⊙	⊙		●	
Liquidambar miocinica Hu *et* Chaney	*L. formosana* Hance		*	+			○	*	⊙	+	○	○	○	+	⊙		○	○	⊙
Quercus miovariabilis Hu *et* Chaney	*Q. variabilis* Blume		*		⊙					+	●	⊙	○		⊙	●	●	●	⊙
Pinus miocenica Tanai	*P. densiflora* Parlatore			+	○		⊙	*	○	+	⊙		+	●		○		⊙	+
Carpinus heigunensis Huzioka	*C. tshonoskii* Maximowicz			+	○	○	+		+	+	⊙	+	○	○		○	○	○	+
Cyclocarya ezoana (Tanai *et* Suzuki) Wolfe *et* Tanai	*C. paliurus* Iljinskaya			○	+		○			+		○	+		●				⊙

	Keteleeria ezoana Tanai	*K. davidiana* (Bertrand) Beissner	+	+	⊙			+	⊙	○	⊙	+	+	⊙	○	⊙	+
e	*Camellia protojaponica* Huzioka	*C. japonica* L.	+		+		+	+		+	○	⊙					
	Ulmus carpinoides Goeppert	*U. davidiana* Planchon		+			○							⊙	●		○
	Diospyros miokaki Hu *et* Chaney	*D. kaki* Thunberg			+		○		+	○		●				+	+
e	*Cyclobalanopsis* Oerst spp.					∗	○	○	⊙	+	⊙	●		○	+	●	+
e	*Actinodaphne* Nees spp.					∗	+			○					○		+
e	*Cinnamomum* Schaeffer spp.	*C. camphora* (L.) Siebold				∗	○	+	○	○	○	+	⊙	○	+	+	
e	*Machilus* Nees spp.					∗	○	+	○	○	○	⊙			+	○	
	Libocedrus notoensis (Matsuo) Ishida	*L. formosana* Florin					○		⊙	+	⊙	⊙		⊙		+	
	Cunninghamia protokonishii Tanai *et* Onoe	*C. konishii* Hayata					+	+			+	+		○	+	○	
e	*Castanopsis miocuspidata* Matsuo	*C. cuspidata* (Thunberg) Schottky					+	+			+	○		○		○	

Legend: e: evergreen broad-leaved taxa, ●: very abundant (more than 11%), ⊙: abundant (4–10%), ○: common (1–3%), +: rare (less than 1%), ∗: uncounted data.

Table 2-3. Occurrence of selected fossil plants from the late Miocene (11–6 Ma) (after Momohara, 1997) with and identification of the type of sedimentary basin the fossils are preserved (locality numbers are same as Figure 2-4)

Fossil taxa	Extant relatives	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Betula miomaximowicziana Endo *ex* Tanai	*B. maximowicziana* Regel		○		+	●										
Cryptomeria miyataensis Huzioka *et* Uemura	*C. japonica* (L. fil.) D. Don		+	○		⊙										
Picea spp.		○	+	○	+	⊙									+	+
Acer palaeodiabolicum Endo	*A. diabolicum* Blume *ex* K. Koch		⊙	+		+							●	○		
Betula protoglobispica Tanai *et* Onoe	*B. ermanii* Chamisso	⊙		+	+			○					+	○	+	+
Abies spp.		○	+	○	+	○			+					○	+	○
Fagus protojaponica Tanai *et* Onoe	*F. multinervis* Nakai	●	●	⊙	⊙	+		○		+		○		+	+	
Castanea miocrenata Tanai *et* Onoe	*C. crenata* Siebold *et* Zuccarini		+		○	+					+	○	+	⊙	○	⊙
Ulmus protojaponica Tanai *et* Onoe	*U. japonica* (Rehder) Sargent	⊙	+	○		+	+	○	○	○	+	○	○		○	+
Salix spp.		⊙	+	+	+	●	⊙	○	○	●	⊙				+	
Populus spp.		○	⊙	+	○	●	⊙	+		+	○	⊙	+	○	○	
Carpinus heigunensis Huzioka	*C. tschonoskii* Maximowicz	○	○	○	+		+	○		○	+	○	+	○	○	⊙
Fagus stuxbergii (Nathorst) Tanai	*F. hayatae* Palibin	+	●	●	●	+	●	●	○	○		○	●	●	●	○
Zelkova ungeri (Ettingshausen) Kovats	*Z. serrata* (Thunberg) Makino	○	○		○	+	○	○	○	○	○	○	●	○	○	○
Wisteria fallax (Nathorst) Tanai *et* Onoe	*W. floribunda* (Willdenow) De Candolle	+	○	○	○		⊙	+	○	+	⊙	○	⊙	○	+	
Liquidambar spp.		+			○		⊙	○		○	○	○	○			
Alnus miojaponica Tanai	*A. japonica* (Thunberg) Steudel	+					●	+	○	⊙	⊙			○	+	
Cinnamomum spp.	*C. camphora* (L.) Siebold	+		+	+		+	+	○	+	○	⊙				
Acer rotundatum Huzioka	*A. mono* Maximowicz		○	○	○	○		○		+	○		○	○	○	

	Banbusites-Sasa			⊙		○		⊙	○	●	○	⊙	○			○	
	Quercus protoaliena Ozaki-*Q*. *miocrispula* Huzioka	*Q. aliena* Blume-*Q. crispula* Blume		○	○				○		+	+	○	+	●	+	●
	Acer nordenskioeldi Nathorst	*A. palmatum* Thunberg		+	+			○	○	○	○	+	⊙	○		○	○
e	*Buxus protojaponica* Tanai *et* Onoe	*Buxus microphylla* Siebold *et* Zuccarini		○	○				+			⊙			○	+	
	Tilia spp.				+	+	○	○	○	+	+	○	⊙	○		○	⊙
e	*Cyclobalanopsis* Oerst spp.				○	○			+	○		○	⊙			+	
	Metasequoia occidentalis (Newberry) Chaney	*M. glyptostroboides* Hu *et* Cheng				○		○	+	⊙	○	●				○	
	Quercus miovariabilis Hu *et* Chaney	*Q. variabilis* Blume				○			⊙	+	⊙	+					
e	*Persea cf. thunbergii* Siebold *et* Zuccarini	*P. thunbergii* Siebold *et* Zuccarini							+	○		+	○				
			A	**I**	**I**	**I**	**I**	**A**	**A**	**A**	**A**	**A**	**I**	**I**	**I**	**I**	**I**

Legend: e: evergreen broad-leaved taxa, ●: very abundant (more than 11%), ⊙: abundant (4–10%), ○: common (1–3%), +: rare (less than 1%); **A**: sedimentary basin with developed flood plain; **I**: small sedimentary basin with lacustrine sediment.

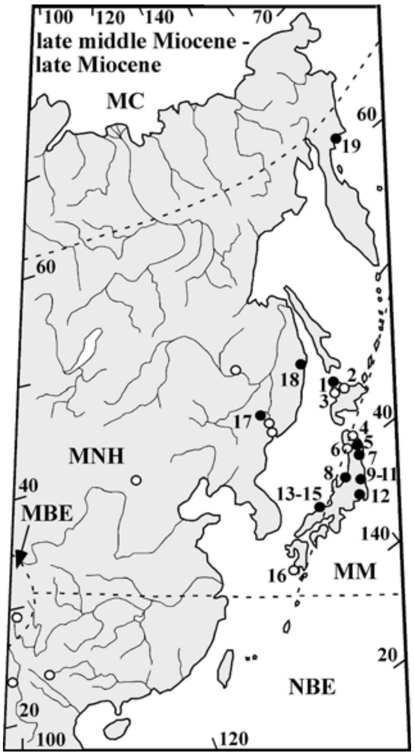

Figure 2-4. The distribution of *Metasequoia* fossils in the late middle Miocene to late Miocene vegetation zones of Japan and eastern Asia. Abbreviations of the vegetation zones (Tanai, 1992) are MM: Mixed Mesophytic Forest; MBE: Microphyllous Broad-leaved Evergreen Forest; MC: Mixed Coniferous Forest; MNH: Mixed Northern Hardwood Forest and NBE: Notophyllous Broad-leaved Evergreen Forest. Closed circle (●) = *Metasequoia* is present and an open circle (○) = *Metasequoia* is absent. The ages of the fossil localities are based on Huzioka (1972), Biske (1975), Fotyanova (1988), Varnavskii *et al.* (1988), Tanai (1992) and Liu *et al.* (1996). Locality data other than 1 (Bifuka—Hotoku—Tanai *et al.*, 1981), 17 and 18 (Lake Khanka and Botchi River, respectively—Varnavskii *et al.*, 1988) and 19 (Korf—Chelebaeva, 1978 are based on Momohara (1997) (Tables 2-2 and 2-3). Localities include the following: 1. Bifuka—Hotoku; 2. Syanabuchi; 3. Tayama; 4. Miyata; 5. Gosho; 6. Sanzugawa; 7. Takamine; 8. Sashikiri; 9. Lower Itahana (including Hanataka site); 10. Upper Itahana; 11. Yagii; 12. Seto; 13. Mitoku; 14. Onbara; 15. Tatsumitoge and 16. Nakayama.

correlated strata from central Japan (Locality 12, Figure 2-4). *Metasequoia* was also absent in 13 fossil assemblages from a small early late Miocene basin from the same region (Momohara & Saito, 2001).

During the late Miocene of Japan, the distribution of plants depended considerably on the topographic setting of the sedimentary basins as suggested by Uemura (1988). Fossil plant-bearing deposits in northern Japan were divided into two groups as well as those in central and western Japan (Table 2-3).

One group is composed of tuffaceous lacustrine sediments that are often interfingered with pyroclastic rocks and talus-like conglomerates at the marginal parts of basin. This type of deposit developed in small subsiding basins that were located along the volcanic zone. Fluvial sediments that grade upward from basal marine to lignite-rich Pliocene deposits indicate marine regressions and characterize the other type of deposit. The fossil floras preserved in the former lacustrine deposits are generally rich in constituents that are found growing in slope and montane forests such as *Cryptomeria* D. Don and *Betula* and sometimes represents vegetation influenced by volcanic activities (Uemura, 1988). *Metasequoia* is more common in the fluvial deposits and occurs with other wetland plants such as *Alnus miojaponica* Tanai and *Glyptostrobus* (Table 2-3).

In the early Pliocene, the coastal plain expanded into central and northern Japan and wide inland basins developed in the eastern and western regions of central and southwestern Japan (Figure 2-5). Most of fossil assemblages from the Plio-Pleistocene strata were obtained from inland fluvial deposits. *Metasequoia* is more common in these deposits than it was during the late Miocene and often dominates the fossil assemblages. The northern limit of

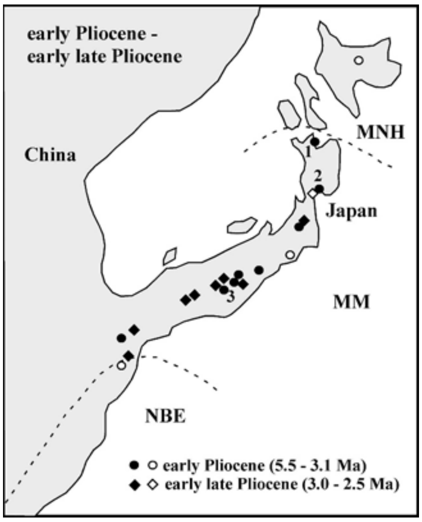

Figure 2-5. The distribution of *Metasequoia* fossils in Japan in the early Pliocene and early late Pliocene with the vegetation zones reconstructed from fossil assemblages in the early Pliocene. The distribution of land and sedimentary basins are based on Ogasawara (1994) and Kimura (2002). Abbreviations of the vegetation zones (Tanai, 1992) are MM: Mixed Mesophytic Forest; MNH: Mixed Northern Hardwood Forest and NBE: Notophyllous Broad-leaved Evergreen Forest. Closed circle (•) and diamonds (♦) = Metasequoia is present, open circle (○) and diamond (◇) = Metasequoia is absent. The localities are as follows: 1. Sarumaru (Kitamura *et al.*, 1972); 2. Sendai (Okutsu, 1955) and 3. Shidatani and other localities included in the Ueno and Shimagahara Formations of the Kobiwako Group (Miki, 1948).

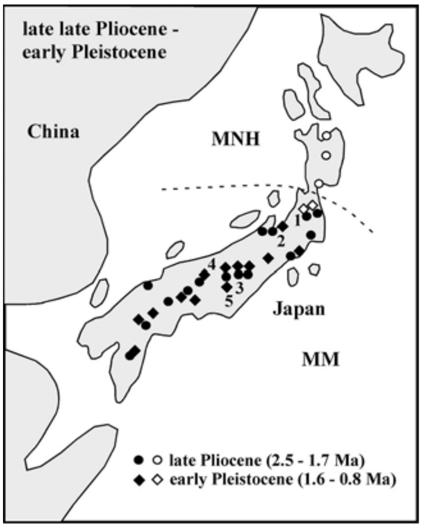

Figure 2-6. The distribution of *Metasequoia* fossils in Japan in the late late Pliocene and early Pleistocene with the vegetation zones reconstructed from fossil assemblages in the late late Pliocene. The distribution of land and sedimentary basins are based on Ogasawara (1994) and Kimura (2002). Abbreviations of the vegetation zones (Tanai, 1992) are MM: Mixed Mesophytic Forest and MNH: Mixed Northern Hardwood Forest. Closed circle (●) and diamonds (◆) = *Metasequoia* is present, open circle (○) and diamond (◇) = *Metasequoia* is absent. The localities are as follows: 1. Aizu (Manabe & Suzuki, 1988); 2. Uonuma (Niigata Fossil Plant Research Group & Niigata Pollen Research Group, 1983); 3. Echigawa fossil site and other localities included in the Ayama, Koga, Gamo and Kusatsu Formations of the Kobiwako Group (Miki, 1948; Yoshikawa *et al.*, 1993); 4. Localities of the lowermost and lowerpart of the Osaka Group (Miki, 1948; Itihara, 1961; Momohara, 1992; Momohara & Mizuno, 1999) and 5. Hashimoto (Miki, 1948).

the distribution of *Metasequoia* in the early Pliocene was recorded in Aomori Prefecture from northernmost Honshu (Locality 1, Figure 2-5).

Between the late Pliocene and the latest early Pleistocene (3.0 to 0.8 Ma), many plants became extinct in central Japan (Momohara, 1994). This extinction was accompanied by climatic deterioration that is indicated by a decrease in the number of subtropical plants. Between the late Pliocene and early Pleistocene, the northern limit of distribution of *Metasequoia* gradually retreated to the south. In Sendai the last occurrence of *Metasequoia* is in the late Pliocene (1.7 Ma) Aizu locality (Okutsu, 1955; Locality 2, Figure 2-5; Manabe & Suzuki, 1988; Locality 1, Figure 2-6), while in Uonuma, the genus persisted until about 1.3 Ma (Niigata Fossil Plant Research Group & Niigata Pollen Research Group, 1983; Locality 2, Figure 2-6).

Plant macrofossil assemblages representing a cool phase during the early Pleistocene are indicated by an absence of warm temperate taxa that were always present in the Pliocene assemblages (Momohara, 1994). During this cool phase, *Metasequoia* occurred together with abundant cool-temperate and subarctic taxa such as *Picea jezoensis* (Siebold *et* Zuccarini) Carrière and *P. maximowiczii* Regel. A fossil assemblage preserved in a backmarsh deposit assigned to the Osaka Group (ca. 1.7 Ma) includes *Metasequoia* and *Picea maximowiczii* together with abundant wetland herbaceous plants (Momohara, 1992). The occurrence and composition of the assemblage indicates that a cool-temperate *Picea* forest was developing in the northern part of the cool-temperate zone that surrounded a *Metasequoia*-dominated wetland forest.

In the upper part of the early Pleistocene, cycles of marine sediments and fluvially deposited gravel of the Osaka Group (Locality 4, Figure 2-6) represent greater climatic and sea-level fluctuations. The uppermost occurrence of *Metasequoia* is recorded in the Ma 2 Marine Clay Layer in the Osaka Group that is correlated with the oxygen isotope stage 23–25 (Yoshikawa & Mitamura, 1999). *Metasequoia* does not occur in the upper horizon of cold stage 22, which is recognized as a glacial stage at the “mid-Pleistocene transition” to the intense later Pleistocene glacial-interglacial cycles.

The late early Miocene fossil records of *Metasequoia* outside of Japan indicate that the genus was widely distributed throughout the Mixed Northern Hardwood Forest zone that included the Mammoth Mountain locality along the Aldan River (Locality 19, Figure 2-3; Dorofeev, 1969), North-Pekul’neyveem locality in the lower reaches of the Anadyr River (Locality 20, Figure 2-3; Nikitin, 1979), Sakhalin, Amur, Sikhote Alin and northeastern China. The distribution also extended to the south along eastern China to Ninghai in Zhejiang Province (Locality 20, Figure 2-3; Liu *et al*., 1996) where Notophyllous Broad-leaved Forests dominated and Shihting in Taiwan (Locality 21, Figure 2-3), which is the northern limit of Paratropical Rain Forest (Tanai, 1992). The late middle and earlier late Miocene localities were limited to three reports: the eastern shore of the Lake Khanka (Locality 17 in Figure 2-4) and the Botchi River site (Locality 18, Figure 2-4); the Sikhote Alin region (Varnavskii *et al*., 1988) and Korf Bay (Locality 19, Figure 2-4) in the Kamchatka region (Chelebaeva, 1978; Blokhina, 1995). These localities represent the uppermost occurrence of *Metasequoia* fossils in East Asia, except for Japan.

4. EXTINCTION AND SURVIVAL OF *METASEQUOIA* IN EAST ASIA

The local extinction of *Metasequoia* in the late Cenozoic has been often attributed to climatic cooling (Hu, 1980; Yang & Jin, 2000). However, the distribution of *Metasequoia* has always extended far over the northern limit of warm-temperate evergreen broad-leaved trees in the Cenozoic of eastern Asia.

Survival in the Oligocene polar regions and its occurrence with cool-temperate conifers in the early Pleistocene of Japan indicates that *Metasequoia* possessed the physiological requirements to tolerate cool temperate climates (Vann, this volume; Williams, this volume). Extant *M. glyptostroboides* Hu *et* Cheng grows near the northern limit of the cool temperate zone in central Hokkaido where January mean temperature is about −5°C (Momohara, personal observation). Freezing experiments by Sakai (1971) indicate that *Metasequoia* can tolerate temperatures down to −30°C. Severe sub-arctic winter conditions possibly exterminated *Metasequoia* populations from northeastern China and the Far East of Russia during the late Miocene. However, their extinction from southwestern Japan cannot be explained simply by climatic cooling because the climate during the Pleistocene of Japan was mild enough for many other Tertiary relicts including *Cryptomeria* to survive.

Aridity however, appears to have limited the distribution of *Metasequoia* throughout the Cenozoic. Records of *Metasequoia* from the Tertiary of East Asia were confined to sedimentary basins near the Pacific Coast and are absent from inland China. Fossil assemblages from the Eocene of central and eastern China are represented by Semi-arid Sclerophyllous Forest (Tanai, 1992) and *Metasequoia* is absent from these areas (Figure 2-1). The distribution of *Metasequoia* expanded from eastern China, south to the northern part of Taiwan in the late early Miocene (Figure 2-3) when the mild maritime climate was dominant with expansion of the sea along the Pacific coast. Summer droughts associated with the arid subtropical and warm-temperate regions were probably unfavorable for the growth of *Metasequoia*. In addition, adequate precipitation in these maritime regions appeared to favor the growth of floral elements such as *Metasequoia*.

The topography of the sedimentary basins also influenced the distribution of *Metasequoia*. Among the late Miocene sedimentary basins in Japan, the distribution of *Metasequoia* was more common in the wide sedimentary basins that formed contiguous fluvial flood plain ecosystems, whereas in the small subsiding basins with lacustrine sediments *Metasequoia* was rare. Fluvial flood plain environments appear to have been more favorable for the establishment of *Metasequoia*. In the smaller basins, *Metasequoia* appears to have been associated with the talus slopes. These small basinal populations were often destroyed by volcanic activity, but the adjacent mountains would have precluded easy exchange with populations from other areas. In central and southwestern Japan, *Metasequoia* was a common constituent of the forests that were associated with the expansion of the flood plain since Pliocene time.

The flood plain habitat of *Metasequoia* was susceptible to orogenic and eustatic events that became more prevalent during the early Pleistocene (Momohara, 1994). The flood plains expanded widely to the east and west in southwestern Japan and became divided into many smaller basins through uplift that extended to the north and south during the late early Pleistocene. Active uplift and orogenies fragmented the alluvial lowlands and began to restrict the movement of *Metasequoia* as climate and sea level changed. The oxygen isotope curves obtained from deep sea drilling cores show that sea-level changes became more prevalent during the late early to middle Pleistocene (Shackleton, 1995). The change of sedimentary facies of central Japan from glacial to interglacial in the Osaka Group also indicates stronger sea-level changes at marine isotope stage 22; a time just after *Metasequoia* became extinct in southwestern Japan. The marine clay beds lower than the Ma2 Marine Clay including fossil *Metasequoia* were deposited continuously in the fluvial silt and clay, but the overlying Ma3 marine clay, which is devoid of *Metasequoia* often possesses inter-fingered sand and gravel (Itihara *et al.*, 1975) that was deposited in alluvial fans. This distribution of sedimentary facies indicates that areas of the alluvial lowlands were limited to transgressions in this interglacial stage (marine isotope stage 21). In addition, the steep topography around the alluvial lowlands hindered the post-glacial migration of the genus, for the dispersal history of *Metasequoia* is different from other Tertiary relicts like *Cryptomeria* and *Sciadopitys* Siebold *et* Zuccarini, which inhabited the forest slopes.

Cold temperatures at the high altitudes may have contributed to reducing the distribution of *Metasequoia* in the Northern Hemisphere. However, it survived until the Plio-Pleistocene in southern Caucasus (Chochieva, 1975) despite increased aridity in central Asia and global climatic deterioration that began during the late Miocene. In the circum-Pacific temperate regions where *Metasequoia* was commonly growing under maritime climate conditions during the early Miocene, the topography in and around the sedimentary basins changed through orogenic events and volcanic activity that began during the late Miocene. These changes culminated in the Plio-Pleistocene and strongly influenced the distribution of *Metasequoia* in the alluvial lowlands and affected migration between the sedimentary basins. The initiation of the Asian monsoon began in the late Miocene and changed the disturbance regimes in the alluvial plains, which likely influenced to the distribution of the plants growing there.

There is no fossil evidence that records the survival of *Metasequoia* in central and southern China during the Plio-Pleistocene because of the scarcity of plant fossil beds in the Yangtze Valley. The series of sedimentary basins and flood plains in southwestern Japan are assumed to have continued to the south to a subsidence zone located along the eastern margin of the East China Sea (Kimura, 2002). The lower reaches of the Yangtze River extended east to the present day Ryukyu Islands and a vast alluvial lowlands expanded over the area of the current East China Sea prior to the late Pliocene and during the Pleistocene glacial stages. These areas, along with inland basins in the middle reaches of the Yangtze River, may have produced refugia of *Metasequoia* during the Pleistocene glacial stages.

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Chapter 3

A High-Resolution Palynological Analysis, Axel Heiberg Island, Canadian High Arctic

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Abstract: A high-resolution sampling protocol was used to study the microflora from a two-meter thick siltstone unit located between two prominent coals representing *Metasequoia*-dominated swamp forests from the middle Eocene (ca. 45 million years old) Buchanan Lake

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Formation at Napartulik, Axel Heiberg Island, Nunavut, Canada. This detailed analysis facilitated the reconstruction of the local vegetation history and provided possible explanations for the changes seen in the local shifting vegetation patterns. These changes are likely due to two phenomena: environmental disturbances, such as flooding and/or climate change and floral succession. Members of the Pinaceae dominated the local flora at times when the area was relatively dry, whereas *Metasequoia* Miki was predominant when local environmental conditions were more mesic. The pollen data provide evidence of successional processes and suggest that the local vegetation responded to climatic and environmental changes. More importantly, the pollen data indicate that the local floodplain vegetation was part of a larger, dynamic floral mosaic within a regional polar broad-leaved deciduous forest community and that periods of prolonged environmental stasis were generally limited to the swamp forest communities. Two major fern spikes were identified in the sequence and large-scale flooding was identified as being the likely disturbance factor responsible for landscape level reorganization.

Key words: broad-leaved; deciduous; forests; climate; fern spike; *Metasequoia;* Napartulik; Nunavut; paleoecology; palynology; polar; pollen; spores.

1. INTRODUCTION

In a previous study, McIntyre (1991) identified the major pollen and spore taxa that comprised the microflora of the middle Eocene fossil forests at Napartulik (Inuk name for ‘the place of trees’), on eastern Axel Heiberg Island, Canadian High Arctic (Figure 3-1). Seventy samples were collected at random intervals from a 238-meter thick section (McIntyre, 1991). While this time-averaging approach worked well for characterizing the general composition of the vegetation and relative age of the flora, it precluded recognition of high-resolution details such as the ecological and environmental patterns and processes that took place on biological time-scales in this high-latitude environment.

The initial objective of this study was to determine whether a sufficient number of plant microfossils were preserved in the non-coaly facies at Napartulik to conduct a high-resolution (centimeter scale) palynological study. Preliminary data indicated that the microflora was sufficiently diverse and abundant. Therefore, the second objective was to examine in greater detail whether successional trends or regional patterns in the vegetative composition could be detected. The fossils were collected from a two-meter thick section of siltstone located between two prominent coal layers representing *Metasequoia*-dominated swamp forest communities. The results of this study are presented and the resulting vegetation patterns were used to determine whether natural successional processes and/or physical perturbations such as floods caused local changes in the vegetation and forest community over time.

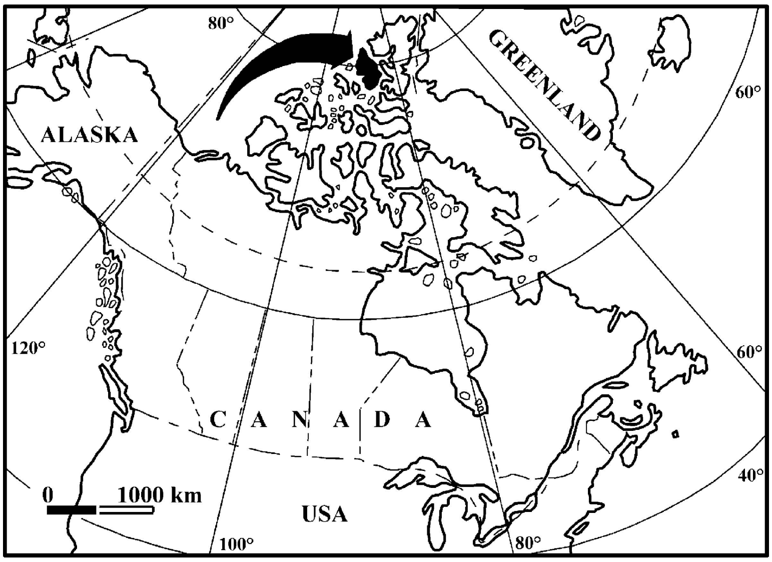

Figure 3-1. Map of Canada showing the location of Axel Heiberg Island, Nunavut (arrow) in the Canadian High Arctic.

2. STUDY AREA

The samples were collected at four-centimeter vertical intervals from a siltstone unit that cropped out between two prominent coal seams. This unit is associated with the Upper Coal member of the Buchanan Lake Formation, Eureka Sound Group, at Napartulik, Axel Heiberg Island, Nunavut, Canada (Figures 3-1 and 3-2; 79°55'N, 89°02'W; Geological Survey of Canada, Map 1301A, Strand Fiord, District of Franklin, 1:250,000). Ricketts (1986, 1991, 1994) described the Buchanan Lake Formation as consisting of four lithologically distinct and mappable members. The microfossils occurred in Ricketts's Upper Coal member, which consists of interbedded sandstone, siltstone and lignite arranged in fining upward sequences. Based on vertebrate remains, structural, petrographic, stratigraphic and palynological features, the Buchanan Lake Formation has been determined to be middle Eocene in age (Lutetian/Uintan (41.3–47.5 Ma); Ricketts, 1986, 1987, 1994; Ricketts & McIntyre, 1986; McIntyre, 1991; Eberle & Storer, 1999; Harrison *et al.*, 1999).

The siltstone (*sensu* Ricketts's (1991) "siltstone-coal (paleosol) association") is approximately two meters thick and located between the prominent Level N and O coals (Figures 3-3 and 3-4). Ricketts (1991) suggested that the siltstone-coal facies represent crevasse splay and floodplain deposits that were located adjacent to sandy meandering river channels that flowed from

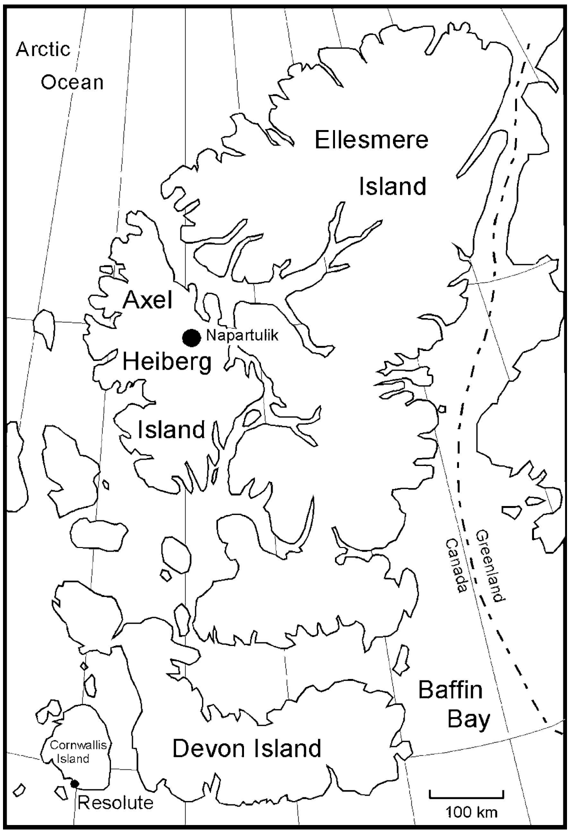

Figure 3-2. Location of Napartulik on eastern Axel Heiberg Island, Nunavut, (79°55'N, 89°02'W), Arctic Canada.

the east to the southwest through a lowland swamp setting. Macrofloral elements previously identified from the Level O coal indicates a swamp forest community that was dominated by *Metasequoia* Miki, with minor amounts of *Picea palustris* LePage, *Pinus* L. and *Pseudolarix amabilis* (J. Nelson) Rehder. The transition from the Level O coal to the overlying siltstone is sharp and abrupt.

The overlying Level N coal was also dominated by *Metasequoia* and contained minor amounts of *Pseudolarix amabilis, Pseudolarix wehrii* Gooch, *Chamaecyparis eureka* Kotyk, *Larix altoborealis* LePage *et* Basinger, *Glyptostrobus* Endlicher, *Pinus* and several unidentified conifer, pteridophyte and angiosperm taxa (Basinger, 1991; Kotyk *et al.*, 2003; LePage, 1993, 2001, 2003a; LePage & Basinger, 1991, 1995). The transition between the siltstone and the overlying Level N coal is also sharp.

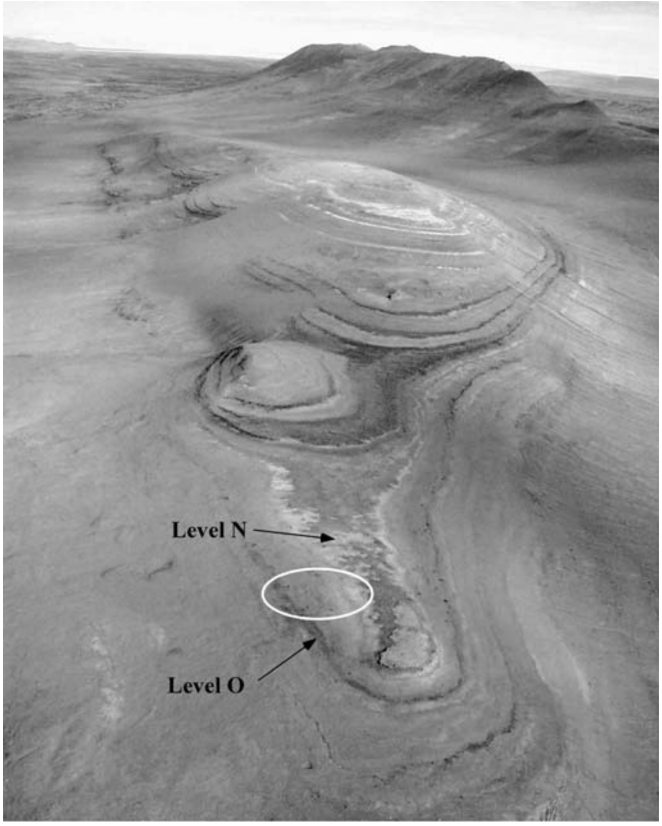

Figure 3-3. The approximate location of the sampling site (ellipse) between the Level N and O coal layers at Napartulik, eastern Axel Heiberg Island. Aerial photograph taken by Christopher King.

3. METHODS

To ensure that the samples were not contaminated, approximately 30 centimeter of surface scree was removed between the Level N and O coals until the permafrost was encountered (Figure 3-4). The resulting trench was then covered with plastic until the permafrost had thawed to allow a sufficient amount of siltstone to be sampled. After four days the top five centimeters of sediment was removed and discarded so that fresh unexposed sediment could be sampled. Fifty samples were collected over the exposed two-meter section of siltstone at four-centimeter vertical intervals. No erosional unconformities or paraconformities were observed throughout the two-meter section during the sampling effort. Therefore, deposition is assumed to have been continuous or nearly so.

Figure 3-4. Open trench showing the location where the samples were collected. Note the stump located at the top of the Level N coal. The Level O coal is at the bottom of the image.

The samples were prepared using the standard procedure of digestion in hydrofluoric (HF) and hydrochloric (HCl) acids, organic matter separation using heavy liquids and oxidation (Traverse, 1988). The samples were prepared by Russ Harms (Global Geolab Limited, 729B 15th Street, Medicine Hat, Alberta, Canada, T1A 4W7). All of the processed samples yielded good pollen and spore assemblages. Approximately 300–500 entire pollen grains and spores per slide were counted. Deteriorated pollen grains and spores were present in all samples and those that could be reliably identified were counted.

Taxonomic identifications were done through comparison with previously published photographs and descriptions of fossils (e.g., Choi, 1983; McIntyre, 1991; McDonald, 1992). Publications providing illustrations and descriptions of extant *M. glyptostroboides* Hu *et* Cheng, *Glyptostrobus pensilis* (Staunton *ex*

D. Don) K. Koch, and species of *Abies* Miller and *Picea* A. Dietrich were also consulted to aid in segregating the fossil pollen grains (Yamazaki & Takeoka, 1956; Ueno, 1974; Sohma, 1985; Soh *et al.*, 1994). The relative pollen percentages based on pollen counts were then calculated for each sample (Appendix A). Once the pollen counts were completed, the percentages were calculated in Tilia^{TM} before being plotted in Tiliagraph^{TM}. The resulting vegetation zones were then determined by visual observations of the plotted data.

4. RESULTS

Major spore and pollen types identified throughout the section included *Laevigatosporites* Ibrahim, *Lycopodium annotinum* L., *Cryptogramma* R. Brown *in* Franklin, *Alnus* Miller, *Pterocarya* Kunth, *Juglans* L., *Quercus* L., *Metasequoia*, *Picea* and *Abies* (Figure 3-5). Minor constituents included *Betula* L., *Carya* Nuttall, *Corylus* L., *Diervilla* P. Miller, *Engelhardia* Leschenault *ex* Blume, *Fagus* L., *Fraxinus* L., *Gothanipollis* Krutzsch, *Ilex* L., Intrapollenites,Intratriporopollenites, *Liliacidites* Couper*, Monocolpopollenites* Kedves, *Nyssa* L., *Pandaniidites* Elsik, *Pinus, Pistillipollenites* Rouse, *Planera* Gmelin, *Polyatriopollenites* Raatz *ex* Potonié, *Salix* L., *Sassafras* Presl *in* Berchtold., *Tilia* L., Triporates, *Ulmus* L. and *Viburnum* L. The minor constituents each represented less than one percent of the total number of angiosperm pollen grains counted in each sample and were not considered any further.

The pollen diagram illustrated in Figure 3-6 is divided into six palynofloral zones (I–VI) and provides an overview of the relative changes in the composition of the local forest vegetation based on the relative abundance of pollen and spores that occurred between two well established *Metasequoia*-dominated swamp forest communities. Among the angiosperm pollen grains that were identified *Alnus* was clearly the dominant taxon in each sample. As such it has been separated from the other angiosperm taxa. *Quercus, Pterocarya* and *Juglans* were the next most abundant genera and they have been grouped and are referred to as the angiosperms. Similarly, *Picea* and *Abies* are the dominant representatives of the Pinaceae and are referred to here as the Pinaceae. The raw data are available and can be requested from the senior author.

The Zone I siltstone flora located immediately above the Level O coal-siltstone contact shows an abundance of angiosperm pollen and low values of Pinaceae and *Metasequoia* pollen. Near the top of Zone I the amount of Pinaceae pollen increases abruptly to 55%, the *Alnus* pollen value drops to 19% and the abundance of angiosperm pollen drops from 50% to 25%. These changes are also coincident with an increase in the total number of spores counted in the samples for this interval.

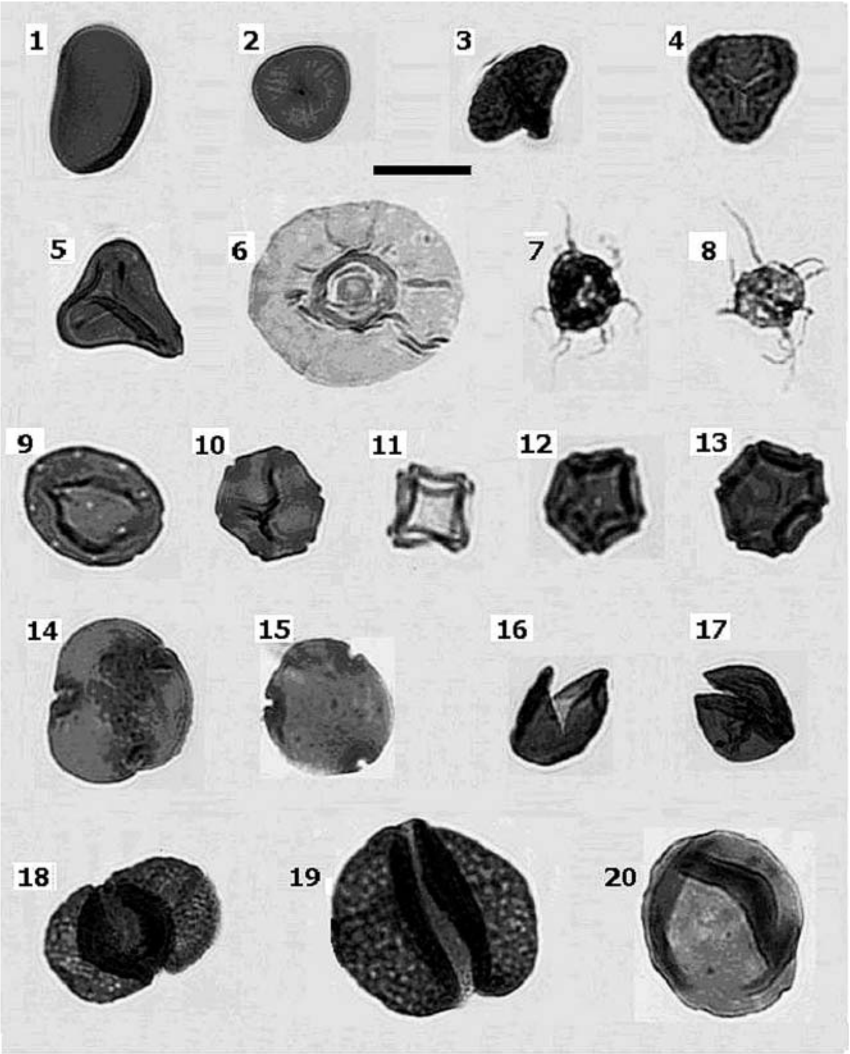

Figure 3-5. A representative assemblage of the microfossils identified from the siltstone outscrop at Napartulik. 1. *Laevigatosporites* sp., 2. *Sphagnum* sp., 3. ?*Cryptogramma* sp., 4. ?*Cryptogramma* sp., 5. *Deltoidospora* sp., 6. *Pterospermopsis* sp., 7. *cf. Micrhystridium robustum* Downie, 8. *cf. Micrhystridium robustum*, 9. *Juglans* sp., 10. *Pterocarya* sp., 11. *Alnus* sp., 12. *Alnus* sp., 13. *Alnus* sp., 14. *Tilia* sp., 15. *Tilia* sp., 16. *Metasequoia* sp., 17. *Metasequoia* sp., 18. *Picea* sp., 19. *Abies* sp., 20. ?*Larix* sp. Bar scale = 100 μm.

In Zone II *Larix* Miller and *Tsuga* (Endlicher) Carrière pollen first appear with each taxon reaching abundances of 25% and 20% respectively in the upper part of the zone. *Metasequoia* pollen values begin to show signs of recovery and the percentage of *Alnus* pollen drops from 25% to 9%. The angiosperm pollen abundances range from 25 to 36% throughout most of the interval and

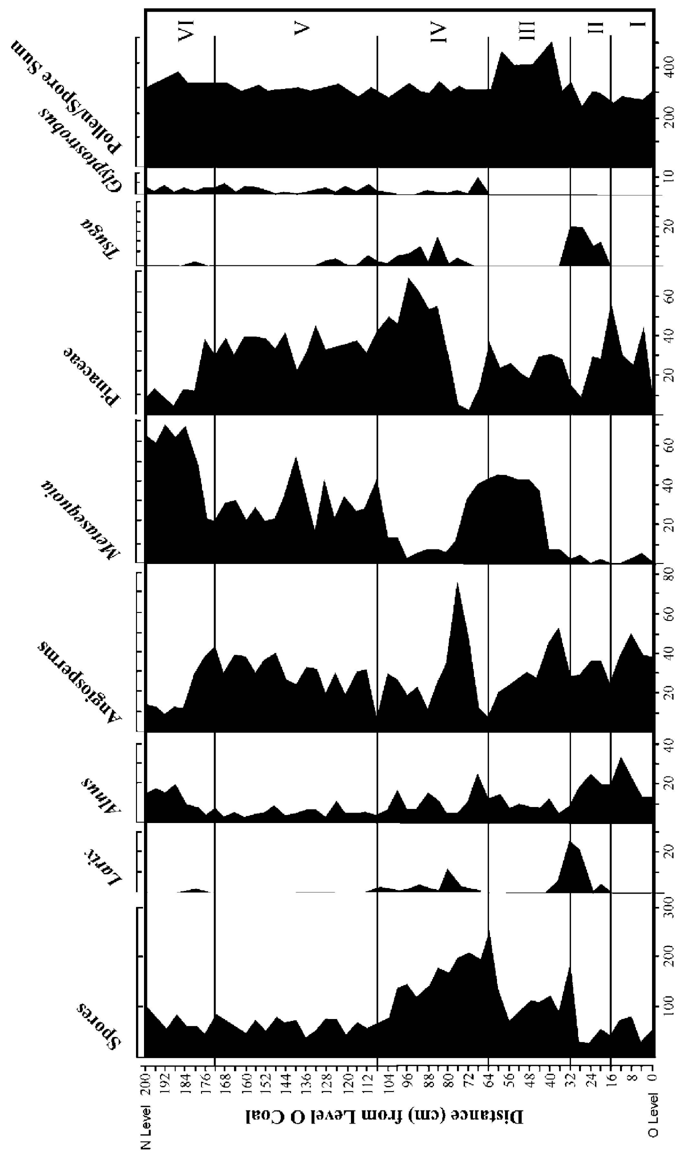

Figure 3-6. Relative changes in the palynoflora through the two-meter section at Napartulik. Major pollen groupings are represented as percentages of the pollen sum. The spore count is the total number of spores counted and was not included in calculating the pollen percentages. Each four-centimeter interval corresponds to one sample.

the Pinaceae pollen values drop from 55% to 9%. The drop in pollen values of *Alnus*, angiosperm and Pinaceae is coincident with the appearance of *Larix* and *Tsuga* pollen. Near the top of Zone II, *Larix* and *Tsuga* pollen values drop sharply and *Alnus*, the angiosperms and the Pinaceae recover as indicated by greater pollen values. At the top of this interval, the first of two major fern spikes is evident. At this point the spores comprised 56.7% of the total number of pollen and spores that were counted.

In Zone III *Metasequoia* becomes a dominant contributor to the palynoflora averaging approximately 40% throughout this interval. *Alnus* pollen values fluctuate between 6 and 14%, the values of angiosperm pollen drop from 53% to 8% and Pinaceae values range from 18 to 36%. *Larix* and *Tsuga* pollen disappear near the base of Zone III. The top of Zone III is marked by the second major fern spike, which accounts for 82% of the total number of pollen and spores counted. At the top of Zone III *Alnus* pollen values show a slight increase in abundance, but *Metasequoia* pollen values begin to drop slightly. The Pinaceae pollen values peak before showing a marked decline at the base of Zone IV and the angiosperm pollen values reach a low prior to recovering in Zone IV.

Following the fern spike in Zone III *Larix* and *Tsuga* pollen re-appear in the section, *Glyptostrobus* pollen first appears and the pollen values of *Alnus*, Pinaceae and *Metasequoia* pollen each drop to below 10%. The abundance of angiosperm pollen increases rapidly to approximately 71%, but then quickly drops as the relative abundance of Pinaceae pollen increases. The recovery of the Pinaceae values approximates that seen in the angiosperms, but it occurs slightly later in time. Nevertheless, the rapid recovery of the Pinaceae pollen appears to have occurred at the expense of the angiosperm pollen values and Pinaceae pollen dominates the palynofloral assemblage throughout Zone IV. Near the top of the zone, *Metasequoia* values begin to recover, *Larix* and *Glyptostrobus* pollen nearly disappear and the abundance of *Tsuga* pollen drops. Although the relative abundance of Pinaceae pollen decreases near the top of this interval, the overall increase in the relative abundance of *Metasequoia* pollen appears to have occurred at the expense of *Alnus* and angiosperm pollen.

Zone V appears to represent a period of ecosystem stability where the relative percentages of *Alnus*, *Metasequoia*, angiosperm and Pinaceae pollen values fluctuate, but remain stable compared to the previous four zones. Changes in the relative abundance of *Metasequoia* pollen appear to correlate well with the changes seen in the angiosperm and Pinaceae pollen values. The percentage of *Alnus* pollen averages about 6% of the total number of pollen grains counted and remains more or less consistent throughout the zone. *Larix* pollen disappears at the base of Zone V and *Tsuga* pollen persists until the middle part of the zone. *Glyptostrobus* pollen appears to follow a cyclic pattern where the relative percentage increases to approximately 5% and then falls to 2–3%. Although Zone V is characterized by a period of ecosystem stability, the middle part of the zone indicates short periods of instability. Here *Metasequoia* pollen values increase rapidly from about 26% abundance to nearly 51% followed by rapid decrease in abundance to approximately 20%. This increase in *Metasequoia* pollen values is correlated to a rapid decrease and increase in the abundance of angiosperm and Pinaceae pollen and the total number of spores. Following this disturbance ecosystem stability appears to return to that seen in the early part of the zone.

Zone VI is characterized by a rapid increase in *Metasequoia* pollen values to a greater than 65% relative abundance. The Pinaceae and angiosperm pollen values fall sharply to 8 and 13% respectively, *Alnus* pollen values increase from about 4 to 19%, while *Larix* and *Tsuga* pollen re-appear, but they each account for about 1% and *Glyptostrobus* pollen accounts for up to 4% of the pollen grains counted.

5. DISCUSSION

5.1. Geology

At Napartulik the Upper Coal member is represented by approximately 400 meters of sediment comprised of sandstone-coal, siltstone-coal and thick sandstone associations. Individual sandstone-coal sequences are commonly 1.5–5.0 meters thick and composed of basal sandstone beds that fine upward into silty-sands and finally into siltstone. The sequence is commonly capped by a coal seam. The siltstone-coal sequences are commonly 0.5–4.0 meters thick and composed of siltstone beds that are usually capped by coal seams. The siltstone-coal and sandstone-coal sequences are most abundant in the lower part of the Upper Coal member and are arranged in a repetitive stack where the basal sandstone or siltstone of one sequence commonly overlies the coal seam of the preceding sequence (Ricketts 1991). More than twenty coal layers are recorded and the thickness of individual coal layers ranges from as little as ten centimeters to more than two meters.

Ricketts (1991) indicated that a broad depositional continuum is represented in the basin in which these deposits accumulated. Alluvial fans emerged from the rising Princess Margaret Mountains that are located to the west of Napartulik. Braided river systems emerged from the valleys located along the mountain front and transported sediment, detritus and plant remains from the montane regions across the floodplain into the lowland regions of the basin. Based on the plant fossils recovered from the channel sand deposits, conifer forests dominated the montane habitats in the Princess Margaret Mountains that were located approximately 10 kilometers to the west of Napartulik. Broad-leaved deciduous forests dominated by members of the Platanaceae, Fagaceae, Betulaceae, Cercidiphyllaceae, Ginkgoaceae, Juglandaceae and Cupressaceae (includes former Taxodiaceae) occupied the floodplain habitats (Basinger, 1991). Distally, these fluvial systems transitioned into meandering river systems that flowed through low-energy *Metasequoia*-dominated swamp forest communities (Ricketts, 1991).

The succession of fining-upwards sequences indicates that periodic flooding, channel migration and crevasse splays are likely responsible for the cyclic sequence of stacked fossil forests seen at Napartulik (Ricketts, 1991). However, the absence of chronostratigraphic controls precludes interpretations on the time that it took for the Upper Coal member or individual siltstone layers to accumulate.

The contact between the Level O coal and the overlying siltstone is sharp, appears to be conformable and indicates that the environment of deposition changed quickly from a swamp to a floodplain environment. Given that the contact between the Level O coal and overlying siltstone remains sharp laterally and is easily identified over several kilometers, the demise of this forest was probably due to a major flooding event. Regardless of the process, the Level O *Metasequoia* forest was killed, buried and subsequently replaced by a broad-leaved deciduous forest. Given the lack of erosional unconformities and paraconformities in the measured section, we have assumed that deposition of the unit was continuous or nearly so. Should a mechanism by which we could reliably date these sediments become available, we could test this hypothesis. Nevertheless, despite our inability to determine the length of time represented by the siltstone layer, Kojima *et al.* (1998) provide an estimate of the accumulation rates for the coals. Based on a leaf lignite accumulation rate of 0.8-mm/year (Kojima *et al.,* 1998), the Level O coal, which is approximately 70 centimeters thick, persisted for at least 875 years and indicates that the *Metasequoia* swamp forest community underlying the measured section was relatively stable, despite being located in a tectonically active foreland basin.

5.2. Palynofloral Assemblages and Paleoenvironmental Reconstruction

5.2.1. Zone I

The palynoflora from Zone I confirm the sedimentological data, which indicates that the change from a swamp to floodplain forest was rapid because the *Metasequoia* pollen disappears within eight centimeters of the contact. The fact that the entire Level O coal is capped by siltstone and evidence that *Metasequoia* disappears soon after the contact, strongly suggests that the Level O forest was killed by large-scale regional flooding. The pollen assemblage identified in the siltstone immediately overlaying the Level O coal indicates that a broad-leaved deciduous flora dominated by *Carya*, *Pterocarya* and *Alnus* was established soon after the *Metasequoia*-dominated swamp forests were eliminated.

The presence of *Alnus* following elimination of the *Metasequoia* swamp forest community was not entirely unexpected. *Alnus* is an early successional genus that is shade intolerant, occupies open alluvial wetland soils and riverbanks and is an aggressive colonizer of these environments following disturbance (Ritchie, 1987; Franklin, 1988). The ability of *Alnus* to form symbiotic actinorhizal associations with the ascomycete *Frankia* Brunchorst enables members of the genus to rapidly colonize and thrive on nutrient poor mineral soils and fresh alluvium (Bousquet & Lalonde, 1990). The simultaneous increase in angiosperm pollen at the base of the siltstone indicates the establishment of a mixed broad-leaved deciduous forest, probably through seed dispersal and encroachment from the adjacent upland habitats.

Although members of the Pinaceae such as *Larix, Pinus, Pseudolarix* Gordon, *Tsuga, Keteleeria* Carrière and *Picea* occur as rare elements in the coal layers, the large number of *Picea sverdrupii* LePage seed cones recovered from point bar deposits in the sandy facies that cross-cut the coals and siltstone units indicates that the spruces were one of the dominant trees growing in the Princess Margaret Mountains located several kilometers to the east of Napartulik (LePage, 2001, 2003a, unpublished; LePage & Basinger, 1991, 1995). The Pinaceae pollen in the overlying Zone I siltstone is dominated by *Picea* and *Abies*. Given that no macrofloral remains of *Abies* have been found in the fossil-bearing siltstone and coal layers, it is also likely that *Abies* was growing as part of an old-growth forest community in the nearby Princess Margaret Mountains together with *P. sverdrupii* and *Tsuga swedaea* LePage. Such forest associates are not uncommon today. In the Cascade Mountains of the Pacific Northwest, *Abies amabilis* Douglas *ex* J. Forbes and *Tsuga heterophylla* (Rafinesque) Sargent forests are extensive and depending on the local climatic and environmental conditions, species such as *Tsuga mertensiana* (Bongard) Carrière, *Larix occidentalis* Nuttall, *Picea engelmannii* Parry *ex* Engelmann, *Pinus contorta* Douglas *ex* Loudon and *Chamaecyparis nootkatensis* (D. Don) Spach can be important associates (Franklin, 1988).

The relative rarity of *Larix, Picea, Pinus, Tsuga* and *Chamaecyparis* Spach compared to *Metasequoia* in the lowland forest communities at Napartulik indicates that these constituents may have been more prevalent in the foothill and montane regions of the Princess Margaret Mountains and occasionally grew as individual or small outlier populations in the lowlands when environmental conditions favored the growth and survival of these taxa. Nevertheless, at the local scale, interpretation of the changes in Pinaceae pollen abundance is difficult given that most of these pollen grains were carried by air or water from the nearly mountains. However, large-scale changes seen throughout our measured section may be relevant for understanding climatic change.

Near the top of Zone I the relative abundance of the angiosperms and *Alnus* decrease and the Pinaceae and spore-producing plants increase, possibly in response to cooling or perhaps local flooding.

5.2.2. Zone II

At the bottom of Zone II the relative abundance of the angiosperm and *Alnus* pollen begins to increase and Pinaceae pollen and spore-producing plants decrease. The Zone II flora is also characterized by the re-appearance of *Metasequoia* pollen and the first appearance of *Larix* and *Tsuga* pollen. The presence of *Larix* and *Tsuga* together in the same deposit is interesting given their ecological requirements. *Tsuga* is the most shade tolerant of all of the genera in the Pinaceae, but it cannot tolerate long periods of drought and grows best where precipitation in the form of rain, snow or fog ranges from 700 to 4500 mm/year throughout the year (Farjon, 1990). In the Pacific Northwest, *T. heterophylla* is one of the main constituents of the old-growth forests at elevations up to 1000 meters, whereas *T. mertensiana* occupies the higher elevations (Franklin, 1988). Alternatively *Larix*, like *Alnus,* is an early successional genus that is shade intolerant and grows well on mineral and alluvial soils and wetlands (Schmidt & Shearer, 1991; Arno & Fischer, 1991). However, Peet (1988) has noted that when old-growth *Tsuga-Abies* forests growing in the Cascade Mountains are subject to disturbance such as fire, *L. occidentalis* is one of the principal early successional species. If the vegetative relationships seen in the Cascade Mountains today hold true for the past, then there can be little doubt that pioneer forests composed primarily of *Larix* occupied the disturbed patches in the *Abies-Tsuga* forests.

Based on the pollen data it appears that local climate shifted from drier to wetter conditions. At this time a wetland comprised of *Larix altoborealis*, *Metasequoia* and *Alnus* sp. was established and nearby, a stand of *Tsuga swedaea* appears to have been present. The wetter conditions were however short lived, for near the top of Zone II the *Tsuga* pollen values drop sharply and the relative abundance of *Larix* and *Alnus* pollen drop considerably. Drier conditions are indicated by an increase in Pinaceae and angiosperm pollen. *Metasequoia* pollen values increase slightly, but the most notable feature at the top of Zone II is the first of two major fern spikes.

5.2.3. Zone III

Drier conditions appear to return during Zone III, as does a *Metasequoia*-dominated forest community. The establishment of *Metasequoia* forest is consistent with the ecology and physiology of the genus. *Metasequoia* behaves much like an early successional plant in that it produces large numbers of small wind-dispersed seeds that germinate well on disturbed alluvial and/or mineral soils and the stand grows quickly as a single cohort (Falder *et al.*, 1999; Vann *et al.*, 2003). Seedling recruitment is limited to open areas because the *M. glyptostroboides* is shade intolerant (Vann *et al.*, 2003). Based on the number of growth rings that could be counted from some of the better preserved *Metasequoia* stumps at Napartulik as well as permineralized stumps of *Metasequoia* from the late Paleocene-early Eocene fossil forests studied at Stenkul Fiord on Ellesmere Island, Nunavut, Canada, these high latitude *Metasequoia* forests may have stood for more than three hundred years (C.J. Williams & B.A. LePage, unpublished).

Near the top of Zone III, the pollen values of all reported taxa drop, while that of the spores increase considerably, indicating that the local area probably suffered from a major flooding event that drowned the local vegetation. The first and second fern spikes account for 56.7% and 81.9% of the total number of pollen and spores counted and indicate that at least local, large-scale environmental change was prevalent. The absence of charcoal in the siltstone and coal layers that have been studied for more that 15 years indicates that fire was probably not a major disturbance factor in these polar environments. In addition, the lack of tipped over tree trunks, eccentric tree stems and flagged treetops among the stems and stumps that are preserved in the coal layers indicate that wind was also not a major disturbance factor (LePage & Williams, unpublished). However, catastrophic flooding due to increased precipitation, possibly melting snow from the mountains (LePage, 2003b) or changes in eustacy provide a reasonable explanation for the changes seen in the local vegetation patterns and the establishment of fern-dominated ecosystems following such major disturbances.

5.2.4. Zone IV

Following the second fern spike the regional landscape appears to have undergone a major re-organization. *Metasequoia* and Pinaceae pollen values drop considerably and the *Metasequoia* floodplain forests and possibly some of the lower elevation montane and foothill spruce forests appear to be replaced with broad-leaved deciduous forest. *Larix* pollen re-appears and indicates that disturbed habitats were available, while the increase of *Alnus* pollen indicates that wetland and/or riverine habitats were also present. The re-appearance of *Tsuga* pollen suggests that parts of the local environment were stable and that the moisture requirements were sufficient to maintain mature *Tsuga* forests.

The appearance of *Glyptostrobus* pollen is also interesting. Today *Glyptostrobus* is rare and endangered and includes one species, *G. pensilis* that is restricted to small populations along the southeastern coast of China. It grows well on waterlogged soils mainly in marshlands and river deltas; however, the ecology and physiology of *Glyptostrobus* still remains poorly understood (Fu & Jin, 1992). Ricketts (1994) indicates that deposition of the Buchanan

Lake Formation was diachronous with depositional events that were occurring at different stages within a number of synorogenic intermontane basins on Axel Heiberg and Ellesmere Islands during the early Eocene or possibly the latest Paleocene. At this time the relative sea-level was high and the depositional environment of southern Axel Heiberg Island (including Napartulik) and west-central Ellesmere Island consisted of a large river-dominated delta plain and alluvial plain complex (Ricketts, 1994). If *Glyptostrobus* preferentially occupied these ancient river-dominated deltas, as is the case today, then the appearance of *Glyptostrobus* at Napartulik might be indicative of highstand conditions and that *Glyptostrobus* periodically migrated upstream to avoid the saline conditions of an encroaching sea so that the delta plain and meanderplain environments were nearly juxtaposed. Interestingly, a small number of acritarchs, which did not appear to be reworked, were found associated with the second fern spike. The presence of marine organisms in a freshwater swamp/floodplain environment reflects an influx of marine elements upstream and warrants further investigation.

Although *Glyptostrobus* persisted throughout Zone IV, its relative abundance dropped, perhaps in response to a relative drop in the sea level. Throughout Zone IV the abundance of the ferns drops, possibly in response to the development of a local forested ecosystem, the lack of suitable habitat or the onset of drier conditions. The increase in Pinaceae throughout Zone IV suggests a return to drier conditions.

5.2.5. Zone V

Although climate in Zone V shows oscillations between wetter and drier conditions, the pollen spectrum indicates a period of relative environmental stability. McIntyre (1991) suggested that a mosaic of plant communities occupied the area of deposition and that one would expect to find a variety of plant communities and possibly evidence of plant successional patterns through time. The microflora of Zone V provides evidence of this mosaic and of reasonably stable vegetation communities shifting in space and in time.

5.2.6. Zone VI

Zone VI marks the return of the *Metasequoia*-dominated swamp forest community and a return to more mesic conditions. Pinaceae pollen values drop considerably, as do those of the broad-leaved deciduous forests. *Alnus* pollen increases indicating that wetland and riverine habitats were becoming more prevalent in the landscape. *Larix, Tsuga* and *Glyptostrobus* pollen persist, but they continue to remain minor constituents in the local landscape. The relative abundance of *Metasequoia* pollen increases from approximately 21% to 66%. At the top of Zone VI the environment changed from a fluvially dominated floodplain characterized by siltstone deposits to a low energy

Metasequoia-dominated swamp where large amounts of organic matter began to accumulate. The Level N coal that overlies the siltstone deposit is approximately one-meter thick and based on Kojima *et al.*'s (1998) leaf lignite accumulation rate of 0.8 mm/year, the environment appears to have been relatively stable for more than 1,200 years.

6. CONCLUSIONS

McIntyre (1991) indicated that despite slight variations in the dominance and abundance of species or the presence/absence of species, there were no discernable patterns in palynofloral change and that the entire 238-meter thick section that was measured at Napartulik represented one biostratigraphic unit. Our data support these conclusions, in part. Although the taxonomic composition throughout our two-meter section remained consistent with that identified by McIntyre (i.e., we found no new taxa), the short-term or biological time-scale patterns became evident based on our centimeter-scale sampling strategy. The results of this study indicate that at least at the local scale, the floodplain vegetation was dynamic and subject to environmental and climatic perturbations and that the vegetation responded to these disturbances, though we are unable to precisely determine the length of time it took for these changes to occur.

The use of a high-resolution sampling protocol to analyze the microflora at this site provides evidence that these polar ecosystems were considerably more dynamic than a coarse sampling resolution would lead us to believe. It has also created the ability to better understand the relationship between vegetational changes due to variations in the site's moisture regime and the change in the floral assemblage due to environmental disturbances. Future studies will hopefully consider the rate of sediment accumulation, as well as the amount of soil compaction that has occurred at this location so that the time it took for the vegetation changes and processes identified in this and other siltstone units can be assessed. Finally, the fern spikes provide evidence of large-scale environmental disturbances. Detailed study of these intervals, as well as the identification of additional spikes in other siltstone units may shed some light on the climatic and sedimentary processes that helped shape these high latitude forests.

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9. APPENDIX A: POLLEN/SPORE COUNTS AND PERCENTAGES ENCOUNTERED AT EACH SAMPLING LAYER

Number	Slide 1	Slide 2	Slide 3	Slide 4	Slide 5	Slide 6	Slide 7	Slide 8	Slide 9	Slide 10	Slide 11	Slide 12	Slide 13	Slide 14	Slide 15	Slide 16
	Zone 1			Zone 2					Zone 3							
Spores	61	27	82	78	42	58	28	32	198	84	126	110	114	94	71	131
Larix	0	0	0	1	8	1	55	53	9	0	0	0	0	0	0	0
Alnus	31	54	64	40	40	59	50	20	9	31	33	32	31	25	47	41
Angiosperms	93	124	75	53	77	85	80	59	80	105	102	105	80	72	67	28
Metasequoia	13	7	0	0	5	1	12	4	10	15	136	147	124	139	154	145
Pinaceae	106	64	60	115	61	69	26	33	43	66	109	63	63	82	83	123
Tsuga	0	1	0	0	24	20	54	43	0	0	0	0	0	0	0	0
Glyptostrobus	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Total w/spores	305	277	281	287	257	293	305	244	349	302	506	457	412	412	422	468
w/o spores	244	250	199	209	215	235	277	212	151	218	380	347	298	318	351	337
Percent	Slide 1	Slide 2	Slide 3	Slide 4	Slide 5	Slide 6	Slide 7	Slide 8	Slide 9	Slide 10	Slide 11	Slide 12	Slide 13	Slide 14	Slide 15	Slide 16
Larix	0	0	0	0	4	0	20	25	6	0	0	0	0	0	0	0
Alnus	13	22	32	19	19	25	18	9	6	14	9	9	10	8	13	12
Angiosperms	38	50	38	25	36	36	29	28	53	48	27	30	27	23	19	8
Metasequoia	5	3	0	0	2	0	4	2	7	7	36	42	42	44	44	43
Pinaceae	43	26	30	55	28	29	9	16	28	30	29	18	21	26	24	36
Tsuga	0	0	0	0	11	9	19	20	0	0	0	0	0	0	0	0
Glyptostrobus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Number	Slide 17	Slide 18	Slide 19	Slide 20	Slide 21	Slide 22	Slide 23	Slide 24	Slide 25	Slide 26	Slide 27	Slide 28	Slide 29	Slide 30	Slide 31	Slide 32	Slide 33
	Zone 4										Zone 5						
Spores	257	198	210	202	173	177	142	124	145	139	76	70	59	70	45	75	78
Larix	0	1	3	14	0	2	4	1	0	1	3	0	1	1	0	0	0
Alnus	14	11	6	7	15	23	11	14	27	12	6	15	12	11	28	8	16
Angiosperms	7	56	70	42	31	21	35	35	52	50	13	74	77	39	75	49	74
Metasequoia	23	39	11	6	10	14	8	4	25	22	86	64	68	69	60	108	40
Pinaceae	8	4	6	36	70	91	89	117	87	84	82	75	96	75	93	87	106
Tsuga	0	6	0	17	0	13	7	8	1	2	8	1	1	5	4	0	0
Glyptostrobus	5	0	2	0	1	4	0	0	0	1	1	12	2	9	2	9	6
Total w/spores	314	315	308	324	300	345	296	303	337	311	275	311	316	279	307	336	320
w/o spores	57	117	98	122	127	168	154	179	192	172	199	241	257	209	262	261	242
Percent	Slide 17	Slide 18	Slide 19	Slide 20	Slide 21	Slide 22	Slide 23	Slide 24	Slide 25	Slide 26	Slide 27	Slide 28	Slide 29	Slide 30	Slide 31	Slide 32	Slide 33
Larix	0	1	3	11	0	1	3	1	0	1	2	0	0	0	0	0	0
Alnus	25	9	6	6	12	14	7	8	14	7	3	6	5	5	11	3	7
Angiosperms	12	48	71	34	24	13	23	20	27	29	7	31	30	19	29	19	31
Metasequoia	40	33	11	5	8	8	5	2	13	13	43	27	26	33	23	41	17
Pinaceae	14	3	6	30	55	54	58	65	45	49	41	31	37	36	35	33	44
Tsuga	0	5	0	14	0	8	5	4	1	1	4	0	0	2	2	0	0
Glyptostrobus	9	0	2	0	1	2	0	0	0	1	1	5	1	4	1	3	2

Number	Slide 34	Slide 35	Slide 36	Slide 37	Slide 38	Slide 39	Slide 40	Slide 41	Slide 42	Slide 43	Slide 44	Slide 45	Slide 46	Slide 47	Slide 48	Slide 49	Slide 50
	Zone 5										Zone 6						
Spores	55	38	75	72	77	56	75	49	63	72	89	46	62	63	82	56	97
Larix	0	1	0	1	0	0	0	1	0	0	0	3	0	1	0	0	0
Alnus	17	17	10	21	15	12	7	12	8	21	10	27	27	51	41	47	30
Angiosperms	84	62	62	94	84	71	93	101	70	110	94	83	32	35	24	34	29
Metasequoia	81	137	79	49	48	65	52	79	69	54	54	133	180	171	198	169	138
Pinaceae	75	52	95	72	84	92	93	71	85	72	86	31	31	12	27	32	18
Tsuga	0	0	0	1	1	0	0	0	1	0	0	2	1	1	0	0	0
Glyptostrobus	2	1	2	1	4	9	9	2	12	8	8	7	7	3	12	3	6
Total w/spores	314	308	323	311	313	305	329	315	308	337	341	332	340	337	384	341	318
w/o spores	259	270	248	239	236	249	254	266	245	265	252	286	278	274	302	285	221
Percent	Slide 34	Slide 35	Slide 36	Slide 37	Slide 38	Slide 39	Slide 40	Slide 41	Slide 42	Slide 43	Slide 44	Slide 45	Slide 46	Slide 47	Slide 48	Slide 49	Slide 50
Larix	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Alnus	7	6	4	9	6	5	3	5	3	8	4	9	10	19	14	16	14
Angiosperms	32	23	25	39	36	29	37	38	29	42	37	29	12	13	8	12	13
Metasequoia	31	51	32	21	20	26	20	30	28	20	21	47	65	62	66	59	62
Pinaceae	29	19	38	30	36	37	37	27	35	27	34	11	11	4	9	11	8
Tsuga	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Glyptostrobus	1	0	1	0	2	4	4	1	5	3	3	2	3	1	4	1	3

Chapter 4

Metasequoia in the Oligocene Bridge Creek Flora of Western North America: Ecological Implications and the History of Research

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Abstract: The early Oligocene Bridge Creek flora of the John Day Formation in Oregon, USA, is an example of the broad-leaved deciduous vegetation that became widespread in the Northern Hemisphere following the Eocene-Oligocene climatic cooling, and demonstrates the significant participation of *Metasequoia* Miki in newly-developing communities analogous to the modern Mixed Mesophytic Forest of China. Before the discovery of living *Metasequoia glyptostroboides* Hu *et* Cheng in China, the Bridge Creek fossils were identified as *Sequoia* Endlicher, which led to erroneous ecological and community composition interpretations of the Bridge Creek

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flora based upon comparisons with the modern redwood forest of California. Soon after the discovery of living *M. glyptostroboides*, paleobotanist Ralph W. Chaney visited the modern *M. glyptostroboides* forest in China in 1948, and this had a major influence on his concepts about the composition and biogeographic history of North American fossil forests. Many of the North American fossils that had previously been assigned to *Sequoia* or *Taxodium* Richard were subsequently reassigned by Chaney to *Metasequoia*. Chaney postulated that the Oligocene deciduous forests such as Bridge Creek had reached the middle latitudes by the "migration" of an intact Arcto-Tertiary geoflora from the higher latitudes, but this concept is no longer well supported. Instead, the Mixed Mesophytic Forest apparently originated through various responses of individual species during the Eocene-Oligocene transition, including 1) extinction or extirpation, 2) pre-adaptation or evolution in place, 3) dispersal from higher elevations, or 4) dispersal from higher latitudes. Extant *M. glyptostroboides* is endemic to a very restricted area in central China, and survival of the few remaining natural stands is doubtful unless new measures are taken to conserve the Mixed Mesophytic Forest as an entire community.

Key words: Arcto-Tertiary Geoflora; Bridge Creek flora; Cedarville flora; Eocene-Oligocene transition; global climate change; John Day Formation; Mixed Mesophytic Forest; Napartulik.

1. INTRODUCTION

Metasequoia Miki is a deciduous conifer in the family Cupressaceae (within which the former Taxodiaceae has been subsumed). The genus was widespread in the Northern Hemisphere during the Cretaceous, Tertiary and Quaternary Periods, although its geographic distribution shifted significantly through time (Yang, 1999, Yang & Jin, 2000; LePage *et al*., this volume). It survives today as a relict within a very restricted range in the Mixed Mesophytic Forest of central China.

One of the significant fossil occurrences of *Metasequoia* is in the Oligocene Bridge Creek flora of the John Day Formation, Oregon, USA. This fossil flora is one of the best examples to show the early development of the type of vegetation in which *Metasequoia glyptostroboides* Hu *et* Cheng occurs today. The Bridge Creek flora represents an important stage in the early origin of Mixed Mesophytic Forest vegetation during the Oligocene epoch. It also illustrates the historical significance of the discovery of living *M. glyptostroboides* on interpretations of western North American fossil floras. The history of the study of *Metasequoia* from Bridge Creek, combined with the discovery of living *M. glyptostroboides* trees in China, had major effects on the development of concepts relating to the interpretation of forest ecology and plant community evolution during the Eocene-Oligocene transition, which was a time of major global cooling. The study of the modern Mixed Mesophytic Forest in China, including the areas in which *M. glyptostroboides* grows, provides important links for interpreting the ecology and forest dynamics of this ancient community.

At Bridge Creek and in many other fossil floras of North America, fossils that later came to be recognized as *Metasequoia* were collected and studied for several decades prior to the discovery of living *M. glyptostroboides* trees in China during the mid-1940s. The misidentification of these fossils as *Sequoia* Endlicher or *Taxodium* Richard led to erroneous conclusions about the floristic composition and evolution of middle Tertiary plant communities in western North America. The discovery of living *M. glyptostroboides* trees in China, however, caught the attention of Professor Ralph W. Chaney of the University of California at Berkeley, who had spent many years studying the Bridge Creek fossil plants. This discovery had a major influence on Chaney's ideas about the composition and biogeographic history of North American fossil forests.

This chapter is intended to provide a review of the fossil record and historical study of *Metasequoia* from the Bridge Creek flora, and to show how the discovery of the living trees influenced interpretations of forest ecology and evolution in western North America. It will also summarize a model depicting the early development of the Mixed Mesophytic Forest vegetation during the Oligocene, and emphasize the importance to paleobotany of preserving the remnants of the similar forest community in which *M. glyptostroboides* survives today. In its modern relictual distribution in China, *M. glyptostroboides* remains a component of the Mixed Mesophytic Forest (Wang, 1961). Efforts to conserve this living forest need to focus beyond the simple preservation of this important species and to recognize the need for preserving this area as a phytoecological community. This community stands as a remnant not only of what remains of *M. glyptostroboides*, but also of what remains of a forest type that began to develop its modern aspect during the Oligocene. The Bridge Creek flora provides important evidence about the origin of this type of forest.

2. *METASEQUOIA* IN THE BRIDGE CREEK FLORA

Metasequoia was one of the most dominant elements in the early Oligocene Bridge Creek flora, which also included such other prevalent plant families such as the Platanaceae, Ulmaceae, Fagaceae, Betulaceae, Juglandaceae, Rosaceae and Sapindaceae (including Aceraceae) (Manchester & Meyer, 1987; Meyer & Manchester, 1997). The flora is comprised of at least nine distinguishable assemblages, each of which is geographically distinct and stratigraphically confined. Throughout the area of its known fossil record, the Bridge Creek flora covers an area of at least 12,000 km^2, and radiometric dates indicate that it spans a period of 1.8 million years with dates ranging from 31.8 to 33.6 million years (Ma) (Meyer & Manchester, 1997). The Bridge Creek flora is one of the best North American examples of the broad-leaved deciduous vegetation that became widespread in the mid-latitudes of the Northern Hemisphere following the Eocene-Oligocene climatic cooling event 33.6 to 34 Ma ago. The flora demonstrates the significance and dominance of *Metasequoia* in newly developing communities that were analogous to the modern Mixed Mesophytic Forest of eastern Asia.

Metasequoia is known at Bridge Creek from foliage, cones, and seeds (Figures 4-1, 4-2 and 4-3). In the early literature, Lesquereux (1883) referred such material to *Sequoia langsdorfii* (Brongniart) Heer, and Newberry (1898) referred it to *Sequoia heerii* Lesquereux. Following the discovery and

Figure 4-1. Metasequoia foliage is one of the dominant components of the Bridge Creek flora, particularly in the assemblage at Twickenham. UCMP-198215. Specimen from the University of California Museum of Paleontology, UCMP-198215. Photograph by Audrey Aronowsky, provided courtesy of Diane Erwin. ©2002 University of California Museum of Paleontology, used by permission.

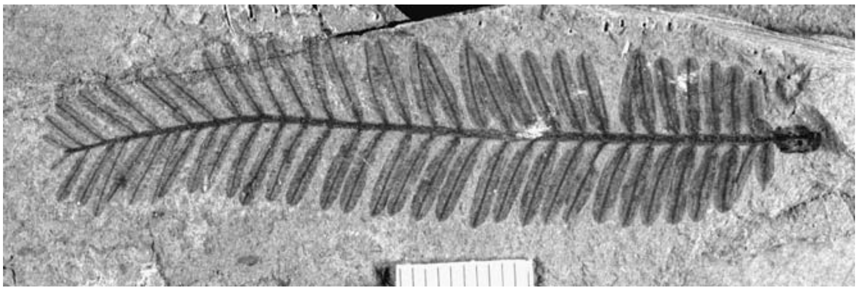

Figure 4-2. Metasequoia foliage from the assemblage at Fossil. Specimen from the University of Florida Museum of Natural History, UF-6990. Scale bar = 1 cm.

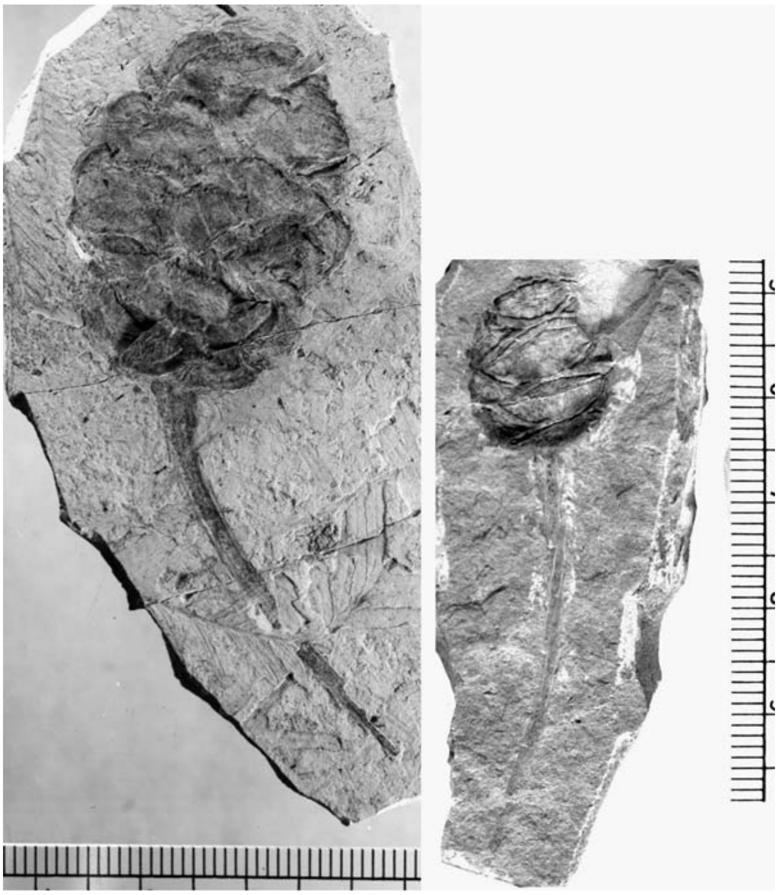

Figure 4-3. Metasequoia cones in the Bridge Creek flora show distinct size differences between different assemblages of the flora. The assemblage at Fossil contains cones that are 2.4 to 3.5 cm in length (shown at left), whereas those in the assemblage at Painted Hills (shown at right) are 1.2 to 1.7 cm. These differences may reflect different habitat types as they do in the modern *Metasequoia* forests, where larger cones are correlated with drought resistant sites and smaller cones are from moister sites. Specimens from the University of California Museum of Paleontology, UCMP-12635 (left) and UCMP-12637 (right).

description of the living *M. glyptostroboides*, Chaney re-assigned many of the North American fossils, including those from Bridge Creek, to *Metasequoia occidentalis* (Newberry) Chaney (Chaney, 1951). However, the type specimen for this species (originally described as *Taxodium occidentale* Newberry from the Paleocene in the state of Washington) has shorter, wider and more apically rounded needles than the typical Bridge Creek specimens. The Bridge Creek material, along with that from other middle Tertiary floras of western North America, appears to have characters that are nearly indistinguishable from modern *M. glyptostroboides* based on foliar and cone morphology, but the lack of epidermal features and cone anatomy makes such an assignment indefinite. Meyer & Manchester (1997) referred the Bridge Creek material to *Metasequoia* sp., noting that a broader study of *Metasequoia* from North American Tertiary floras is needed to resolve some of the remaining nomenclatural problems.

It is noteworthy that the ovulate cones from different Bridge Creek assemblages show distinct size differences (Figure 4-3; Meyer & Manchester, 1997). The most notable difference is between the cones from the assemblage at Fossil (length from 2.4 to 3.5 cm based on 18 specimens) and those from the assemblage at Painted Hills (length from 1.2 to 1.7 cm, based on 14 specimens). These dissimilarities may reflect genetic differences between populations, or they may have been responses to different habitat types. In modern *M. glyptostroboides* forests, trees that produce large cones favor the mountain slope habitat and are more drought resistant, whereas those that produce small cones favor the stream bank habitat and are less tolerant of drought (Li, 1999).

3. HISTORY OF STUDY, EARLY INTERPRETATIONS, AND THE BEARING OF THE DISCOVERY OF EXTANT *METASEQUOIA* ON INTERPRETATIONS OF PALEOCOMMUNITIES

Ralph W. Chaney was an important early contributor both to the study of the Bridge Creek flora and to the study of the modern *M. glyptostroboides* forest. Chaney was a leading American paleobotanist in his time, and had been studying the Bridge Creek flora for more than twenty years when he first learned in 1946 of the discovery of living *M. glyptostroboides* in China. This discovery had a major impact on Chaney's thinking and led to the revision of his interpretation of the Bridge Creek flora and other Tertiary forests of North America.

Prior to the discovery of living *M. glyptostroboides*, the misidentification of the Bridge Creek fossils as *Sequoia* had resulted in erroneous conclusions concerning the community composition and ecology of the flora, and the climate in which it lived. Initially, Chaney (1925) compared the Bridge Creek flora to the modern redwood forest of California. In many respects, Chaney let the identification of one taxon, *Sequoia*, influence and bias his identification of the other components in the fossil flora. At this stage in the history of North American Tertiary paleobotanical studies, fossil identifications were not yet based on rigorous morphological comparative work. Instead, identifications often relied on matching the fossil leaves to superficially similar modern leaf types, with a bias toward the consideration of "ecological probabilities" for the expected presence of particular taxa. Indeed, in his discussion of "principles governing the determination of fossil plants," Chaney referred to the "ecological method" in which comparisons were made with particular modern forests in order "to eliminate the unlikely genera, and at the same time to indicate those genera which should be associated with the known dominants" (Chaney, 1925, p. 6). In applying this method to the Bridge Creek flora, Chaney was misled by his explicit assumption that the fossil flora was dominated by taxa in common with the modern redwood forest, although he did conclude that a minor component of the flora consisted of taxa allied to those now living in eastern Asia, eastern North American, or western Europe (Chaney, 1927). Accordingly, he identified the dominant components of the fossil flora as particular species of *Sequoia*, *Alnus* P. Miller, *Quercus* L. and *Umbellularia* (Nees) Nuttall that had closely related species in the living coast redwood forest (Chaney, 1925, 1927). However, only two of these genera (*Alnus* and *Quercus*) are still considered to be valid identifications in the Bridge Creek flora (Meyer & Manchester, 1997). Chaney's attempt to assess the composition of the Bridge Creek flora by matching its fossil plants with those of the modern redwood forest resulted in a biased taxonomic list that included such other generic misidentifications as *Tsuga* (Endlicher) Carrière, *Philadelphus* L., *Myrica* L., *Corylus* L. and *Asarum* L. All of these misidentifications were the consequence of the misidentification of *Sequoia*, which is what had led Chaney to his comparison with the redwood forest in the first place. Chaney felt assured, however, that "the abundant leaves of *Sequoia langsdorfii* can hardly be referred to any other genus [and] the presence of cones makes certain the generic reference" (Chaney 1925, p. 8). In the circularity of this methodology, it was concluded that the Bridge Creek flora indicated a topographic and climatic setting that was "essentially that of the modern coast range redwood forest which it so closely resembles" (p. 17), although he suggested that the occurrence of fog and the seasonality of precipitation may not have been identical.

Chaney apparently first learned of the discovery of living *M. glyptostroboides* in a letter from H.H. Hu, in which Hu reported "a very important discovery in botany which has some relation to palaeobotany" (letter to Chaney from H.H. Hu, 9 May 1946, Ralph W. Chaney papers, Ax 482, Special

Collections and University Archives, University of Oregon Libraries, cited as UO Archives hereafter; see also Ma, 2003). Hu described W. Cheng's discovery of living trees of *Metasequoia*, a genus which recently had been described by Miki (1941) from the fossil record of Japan. Although in his 1946 letter Hu had proposed the name *Metasequoia sinica* (*nomen nudum*) for the living trees, they later were actually named as *M. glyptostroboides* by Hu & Cheng (1948). Chaney responded to Hu by requesting seeds and remarking that "I consider your discovery one of the most interesting of the century both in botany and paleobotany" (Chaney letter to H.H. Hu, 25 September 1946, UO Archives). Chaney expressed his desire to come to China to see the living trees, but noted "It seems unlikely that I can do so for some time, but I wish that I might" (Chaney letter to H.H. Hu, 14 January 1948, UO Archives). His wish was soon realized only a month later, however, and in February and March of 1948, Chaney became the first American botanist to visit the *M. glyptostroboides* forest (Figure 4-4). His trip was sponsored by the Save-the-Redwoods-League, and he was accompanied by Dr. Milton Silverman, who was the science writer for the *San Francisco Chronicle*, and by C.T. Hwa, a Chinese forester who had previously collected the area's woody flora and had found several hundred *M. glyptostroboides* trees there (Chaney, 1948b). At the time of their visit, the area was even more inaccessible than it is today, and the party walked over steep terrain for five days to reach the Shui-sha-ba Valley (Chaney, 1948c). Although many of the *M. glyptostroboides* trees were observed to be growing as isolated individuals in rice paddies, Chaney did observe what he considered to be relatively natural groves along the borders of the floodplain and up into ravines. He made note of many of the hardwoods growing in association with *M. glyptostroboides*, but because of the late winter season of the visit, he was frustrated by the difficulty in identifying these deciduous associates. Shortly after Chaney's visit, the Metasequoia Preservation Committee was formed and proposals were underway to gain support for the establishment of a Metasequoia National Park (H.H. Hu letter to Chaney, 4 May 1948, UO Archives). Chaney, meanwhile, hoped for another visit to the *M. glyptostroboides* forest later in 1948, "anxious to see these trees when they have their leaves" (Chaney letter to H.H. Hu, 16 June 1948, UO Archives). However, with increasing social and political instability in China by late 1948 and the rise of the communist People's Republic of China in 1949, neither of these objectives came to fruition.

Even before his visit to the living *M. glyptostroboides* forest, Chaney had begun to consider both the taxonomic and ecological implications of this discovery to the Cretaceous and Tertiary floras of western North America. On his return to America, he began a thorough re-examination of the published records for fossil *Taxodium* and *Sequoia* in these floras and re-classified many of them as *Metasequoia*. This work culminated in a monographic revision

Figure 4-4. Professor Ralph W. Chaney of the University of California at Berkeley is shown standing with a Chinese soldier beside the type tree in Moudao during his visit to the *M. glyptostroboides* forest in 1948. Photograph provided by the University of California Museum of Paleontology, courtesy of Diane Erwin.

of much of the North American fossil material (Chaney, 1951), in which he recognized two species, one restricted to the Cretaceous and the other to the Tertiary. He placed the Bridge Creek specimens of *Sequoia langsdorfii* and *S. heerii* into *Metasequoia occidentalis*, which was and generally still is considered to be a widespread species ranging from Paleocene to Miocene in age and from Alaska to California in distribution. Going beyond the taxonomic revision of the fossils, Chaney further realized that the dominant presence of

Metasequoia in many North American fossil floras "calls for reconsideration of the paleoecology and floristics of the Tertiary period," (Chaney, 1948b, p. 509). Still not entirely abandoning the tenets of his earlier "ecological method," Chaney considered that "the need for determining the associates of the living *M. glyptostroboides* becomes at once apparent, for they may represent a closer approach to the Arcto-Tertiary flora [see next paragraph] than any modern vegetation as yet studied." In a reconsideration of the Bridge Creek flora, Chaney realized that "the discovery of *Metasequoia* during the past decade has made necessary an extensive revision of our concepts regarding the Tertiary forests of western North America" (Chaney, 1952, p. 105). He now recognized the close similarity of the Bridge Creek flora to the modern floras of eastern North America and central China, noting particularly the similarity to the flora in the region of the modern *M. glyptostroboides* forest where, "with the exception of *Platanus* L., all of the common Bridge Creek genera are represented by living species...... These modern forests of central China and the eastern United States ... are so similar to the Bridge Creek flora in composition that they provide a sound basis for reconstructing the physical setting in eastern Oregon during the ... Oligocene" (Chaney, 1952, p. 108). Chaney used this modern habitat as the comparative basis to revise the interpretation of the Bridge Creek environment, inferring winter temperatures not much below freezing, heavy summer rainfall and well-drained slopes. He was concerned, however, that past deforestation of the living *M. glyptostroboides* forest might impose limitations on interpreting the entirety of its natural environment.

One of the paleobiogeographical concepts that Chaney embraced throughout much of his career was that of a "migrating" Arcto-Tertiary flora (Chaney, 1938, 1940, 1947, 1948a). It was envisioned that this temperate deciduous flora had originated in high northern latitudes during the Cretaceous and early Tertiary and had moved southward to mid-latitudes in response to cooling temperatures by the Oligocene. During this movement through time and space, the Arcto-Tertiary flora was thought to have maintained much of its floristic identity (of which *Metasequoia* was a dominant component), although Chaney noted that some genera were lost while others were added during the migration of this flora through time (Chaney, 1947). The Arcto-Tertiary flora was thought to have been widespread at high latitudes during the Eocene before its movement southward. Chaney often showcased the Bridge Creek flora as one of the best examples of this Arcto-Tertiary flora in the Oligocene mid-latitudes, where its migration into the region had replaced the earlier subtropical lowland forests. Following his visit to the living *M. glyptostroboides* forest, Chaney inferred the climate of the modern forest by extrapolating climatic data from Chonqing (225 km to the southwest and 1000 m lower), which he then used to infer the climate and physical environment of the deciduous Arcto-Tertiary flora. From this information, he characterized the climate as humid with summer rainfall and having moderate temperatures that rarely fell below freezing (Chaney, 1948a, 1948b). Since Chaney's work, the Arcto-Tertiary model for plant community dispersal has been largely discredited, as discussed below.

Ralph W. Chaney's contributions to studies of the Bridge Creek flora, of living *Metasequoia*, and of the re-evaluation of Tertiary *Metasequoia* fossils and their bearing on Tertiary forest history and ecology were major. Although many of his ideas are no longer supported by more recent evidence from fossil floras or by newer methodologies for studying paleoclimates and the dynamics of community ecology, Chaney's work nevertheless provided an important link in the development of our understanding of the Tertiary forests of North America. In this respect, Chaney exemplified the merits of the scientific process by reevaluating his own ideas based upon new discoveries. Clearly, the discovery of living *M. glyptostroboides* and Chaney's visit as the first American to see it had played a key role to that end.

4. ECOLOGICAL SETTING AND CONSERVATION OF THE MODERN *METASEQUOIA* FOREST

Chaney's study of the modern *M. glyptostroboides* forest was among the first to recognize that many of the American Tertiary floras held strong affinities to the modern forests of Asia, but only limited information about the climate and vegetation of this area was available to him. More recent studies, however, have contributed additional information for understanding the vegetation of China, including the Mixed Mesophytic Forest in which *M. glyptostroboides* is an endemic relictual member (Wang, 1961, Wolfe, 1979). In order to interpret the climate and ecology of fossil floras such as Bridge Creek, it is necessary to first examine the floristic, vegetational and climatic characteristics of the modern Asian forest.

Metasequoia glyptostroboides is confined primarily to the Mixed Mesophytic Forest of western Hubei Province. The Mixed Mesophytic Forest of China is characterized physiognomically by high floristic diversity, a dominance of broad-leaved deciduous taxa, the presence of broad-leaved evergreen and coniferous components, poor stratification below the canopy and entire leaf-margin percentages of 28 to 38 percent (Wolfe, 1979). Floristically, the Mixed Mesophytic Forest is exceptionally rich in species and has the highest diversity of all broad-leaved deciduous forests. Prevalent families include Aceraceae, Betulaceae, Juglandaceae, Rosaceae, Fagaceae and numerous others (Wolfe, 1979). Many relicts are present in this forest type, including such genera as *Cercidiphyllum* Siebold *et* Zuccarini, *Euptelea* Siebold *et* Zuccarini and, of course, *Metasequoia*. In China, Mixed Mesophytic Forest occurs at

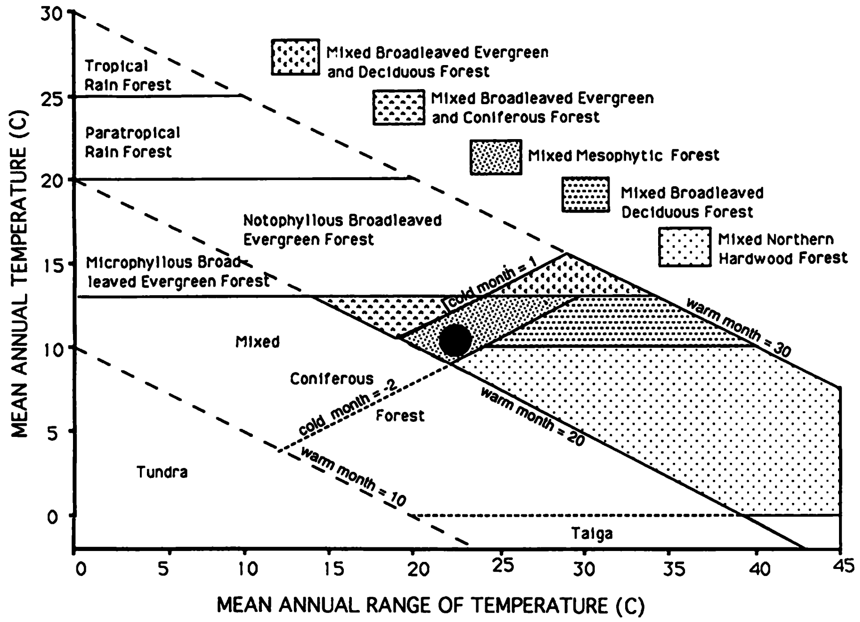

Figure 4-5. The distribution of modern forest types in eastern Asia is determined largely by thermal parameters such as mean annual temperature, mean cold month temperature, mean warm month temperature and mean annual range of temperature. This modern distribution is the basis for inferring the paleotemperatures for the Bridge Creek flora, as indicated by the black circle. Temperature-vegetation diagram based on Wolfe (1978), from Meyer & Manchester (1997).

moderate elevations and has patchy distributions between latitudes 27 and 33°N, extending from near the east coast of China into the central part of the country (see map in Wolfe, 1979). The Mixed Mesophytic Forest occurs under narrowly confined temperature parameters, with the lower elevation limit defined either by a cold month mean temperature of 1°C or a mean annual temperature (MAT) of 13°C, and at the upper elevation limit either by a cold month mean temperature of −2°C or a warm month mean temperature of 20°C (Figure 4-5; Wolfe, 1979).

It should be emphasized that the modern distribution of forest ecosystems in China has been profoundly affected by centuries of human activities such as cutting, fires and clearing to create agricultural lands. The original extent of the natural distribution and composition of Mixed Mesophytic Forest prior to human impact is thus conjectural, and in some areas it must be reconstructed from remnant occurrences (Wang, 1961). Some of these remnants include second-growth forest, or stands within fields that have been cleared for agricultural cultivation, especially along the alluvial plains of the valley bottoms. Sparsely inhabited regions, particularly along the steep slopes, are more likely to preserve remnants of the natural forest, although more detailed ecological site studies are needed to ascertain which of these areas, if any, actually preserve old-growth forest.

In its modern distribution within the Mixed Mesophytic Forest, *M. glyptostroboides* is limited to the riparian habitats of valley bottoms and the moist ravines along the lower slopes of the mountains (Chu & Cooper, 1950, Li, 1964; Williams, this volume), which are settings that are most affected by human activities. Because the living *M. glyptostroboides* trees are restricted to these riparian and lower-slope habitats, and often grow in close proximity to human dwellings, most of the remaining trees are surviving in a highly modified setting that represents only a remnant of the natural Mixed Mesophytic Forest riparian and lower-slope community. This community probably lacks many of its original floristic components, which were lost during depletion of the original forest by human activity (Li, 1964). At some of the sites that we observed during the *Metasequoia* field trip in August 2002, it was difficult to know for certain whether particular *M. glyptostroboides* trees are in remnants of natural stands that have been modified by man, or in stands that have been planted. Large tree size indicating a probable age previous to widespread human habitation of the valley 250 years ago is sometimes the only evidence (without coring) that a tree is naturally occurring. Much of the valley bottom that is presently used for agriculture was probably covered with widespread forests of *M. glyptostroboides* before this human occupation of the area. This is evidenced by large buried trunks that we observed in the valley, and by large isolated trees (such as the type tree at Moudao) that occur some distance from the main Shui-sha-ba Valley (Li, 1964). Although the forest community has been subject to human modification, certain groves apparently were still undisturbed during the time of the discovery of *M. glyptostroboides* in the 1940s (Litoff, this volume). Today, many of the pure stands or isolated trees of *M. glyptostroboides* exist in the valley because they have been cultivated or selectively preserved. The local people who we met in the remote rural villages demonstrate a keen awareness of the importance of *M. glyptostroboides* here. Small, scattered groves that appear to represent relatively natural communities can still be seen (Figure 4-6). The reproductive viability of these few remaining groves is a crucial issue, however, and although tree reproduction was apparently still occurring in the late 1940s (Chu & Cooper, 1950), this was no longer the case by 1980 (Bartholomew *et al.,* 1983).

A "Metasequoia Conservation Committee" was established during the late 1940s (Chu & Cooper, 1950) and plans were underway for the establishment of a "Metasequoia National Park." Although the efforts that followed assured the preservation of many individual *M. glyptostroboides* trees, much of the associated forest community was lost and the objective of establishing a natural preserve or national park was never realized. Now, restoration of the natural

Figure 4-6. This remnant grove of *Metasequoia glyptostroboides* trees grows in a ravine along the slopes surrounding the Shui-sha-ba Valley near Guihua, and was visited on the field trip of the International Metasequoia Symposium in August 2002. Such groves appear to have originated naturally, but it is uncertain whether they remain reproductively viable.

ecosystem is problematical and remains one of the major challenges facing effective preservation of the *entire* forest community to assure viable reproduction of *M. glyptostroboides*. Future efforts need to concentrate on preservation of the Mixed Mesophytic Forest as an ecosystem and to recognize that the survival of *M. glyptostroboides* depends on the survival of this larger plant community.

5. ECOLOGICAL SETTING AND CLIMATE OF THE OLIGOCENE BRIDGE CREEK FLORA

Methods for inferring the ecological setting and community structure of fossil floras has changed since Chaney applied his ecological method to interpreting the Bridge Creek flora in the 1920s. More contemporary methods use either a nearest-living- relative (NRL) approach or a physiognomic approach. The NLR method relies on examination of the modern distribution of similar species, which are inferred from morphological similarity of foliar or reproductive organs between fossil and living organisms. Some applications of the method are qualitative and rely on determining the typical climate shared by the greatest number of taxa that are thought to be nearest living relatives. A more refined application of this method is Mossbrugger's (1999) co-existence analysis in which the temperature ranges for modern nearest-living-relatives are quantitatively plotted, and the interval in which temperature ranges overlap provide the basis for inferring paleotemperature of the fossil flora. In a sense, Chaney's ecological method was a variant of the NLR approach, but his method differed in its explicit preconception that almost all of the relatives of the species in a fossil community could be found in a particular modern community, such as the redwood forest of California. The primary criticisms of the NLR approach are that it relies on valid identification of the fossil material, that modern taxa appearing morphologically similar to the fossils may in fact have evolved other physiological adaptations to tolerate different climatic regimes, that some genera that coexisted in the fossil record are not coincident in their modern climatic ranges, and that workers sometimes give greater weight to some taxa than to others (Spicer, 1990; Wolfe, 1980, 1994).

Whereas the NLR method relies on floristic composition of a flora, the physiognomic approach, by contrast, relies on physical characteristics of the vegetation. These physiognomic characters represent aspects of vegetation that are physical adaptations to particular climates, including the overall taxonomic diversity, the canopy composition and structure and the relative proportions of conifers, evergreen dicots, deciduous dicots, trees, shrubs and lianas. Some of these characters can be observed from fossil leaves, including such features as size, texture, the presence or absence of drip tips and most significantly, the percentage of species that have entire margins (Wilf, 1997; Wolfe, 1978, 1993). Because physiognomic characters of different modern floristic regions show the same relations to climate, it is assumed that a similar correlation has existed throughout the geologic time during which angiosperms and conifers have dominated the world's vegetation. Although floristic groups can evolve through time, the physiognomic characteristics that adapt them to particular climates are thought to have remained stable.

The Bridge Creek flora is clearly similar to the present-day temperate hardwood deciduous forests of eastern Asia and eastern North America. Both physiognomic and floristic criteria indicate that the flora represents Mixed Mesophytic Forest (Wolfe, 1981, Meyer & Manchester, 1997), although not as highly diverse as the modern Mixed Mesophytic Forest seen in Asia. Wolfe (1979) has plotted the temperature parameters for this and other modern forests of eastern Asia based on mean annual temperature (MAT), mean cold month temperature and mean warm month temperature (Figure 4-5). Physiognomically, the leaf margin percentage of 22–35% for various assemblages of the Bridge Creek flora is largely within the range of 28–38% for the modern Mixed Mesophytic Forest, but it also overlaps into the range of 9–24% typical of Mixed Northern Hardwood forest (Meyer & Manchester, 1997). This might indicate that within its geographic range, the Bridge Creek flora was in some areas ecotonal. Other physiognomic similarities to Mixed Mesophytic Forest include the high diversity of taxa, the dominance of deciduous taxa, the relatively minor proportions of conifers and evergreen dicots, the diversity of tree species, the proportion of trees and shrubs to woody climbers and the size classes of the leaves (Meyer & Manchester, 1997). The similarity of Bridge Creek to modern Asian Mixed Mesophytic Forest is also indicated by floristic aspects, including the dominance and diversity of such families as Cupressaceae (including the former Taxodiaceae), Sapindaceae (including the former Aceraceae), Betulaceae, Fagaceae, Hamamelidaceae, Juglandaceae, Leguminosae, Rosaceae, Tiliaceae and Ulmaceae, and the presence of genera now endemic to eastern Asia such as *Metasequoia* and *Cercidiphyllum* (Hu, 1980; Wang, 1961; Wang, 1999). The Bridge Creek flora thus compares favorably with the Mixed Mesophytic Forest, possibly near the transition to Mixed Northern Hardwood forest (a vegetation boundary that exists today in forests in the northern half of Honshu, Japan; see Wolfe, 1979, plate 1; Momohara, this volume).

Certain aspects of the Bridge Creek flora vary from those of the modern Mixed Mesophytic Forest, including an apparently lower taxonomic diversity and a lower proportion of broad-leaved evergreens. The difference in the diversity of broad-leaved evergreens might in part be explained by the higher paleolatitude (48 to 50°N) of Bridge Creek, implying that the flora may have grown under conditions of greater seasonal light variability favoring deciduous taxa, much as modern vegetation shows a sharp decline in broad-leaved evergreens between latitudes 49 and 50°N (Wolfe, 1981). Other differences could be explained by taphonomic factors that biased the preservation of certain plants in the fossil record. The Bridge Creek flora was deposited in lake sediments, and the fossil assemblages therefore favor the representation of valley bottom or lower slope vegetation. The dominance of *Metasequoia* and *Alnus* is therefore not surprising, and the lower proportion of broad-leaved evergreen taxa and the overall lower diversity than modern Mixed Mesophytic Forest might be explained in part by such taphonomic factors as differential preservation of deciduous versus evergreen taxa or proximity of localized habitats to the depositional basin. Another factor that may have influenced the overall floristic diversity is that the regional flora may not have fully recovered yet from the significant climatic cooling that affected the region during the Eocene-Oligocene transition within about a million years prior to the development and origin of the Bridge Creek flora. A further difference with the modern Mixed Mesophytic Forest is the presence of several genera at Bridge Creek that are now extinct (Meyer & Manchester, 1997).

Based on leaf margin percentages, the MAT for Bridge Creek is estimated as 8 to 12°C (Figure 4-5; Meyer & Manchester, 1997). Both floristic and physiognomic aspects of the flora indicate that it evidently represents one of the earliest fossil records bearing a strong similarity to Mixed Mesophytic Forest vegetation.

6. THE EOCENE-OLIGOCENE TRANSITION: CLIMATE CHANGE AND THE DEVELOPMENT OF MIXED MESOPHYTIC FOREST

Another significant aspect of the Bridge Creek flora is that it occupies a critical temporal and spatial position for demonstrating how plant communities of the Tertiary changed in response to global climate cooling during the Eocene-Oligocene transition. The Eocene-Oligocene boundary is now placed at 34 Ma, which may differ from usage in some of the cited earlier literature. The latest Eocene floras of the lowlands in the Pacific Northwest indicate subtropical to marginally paratropical climate that was inhabited by dominantly broad-leaved evergreen forests analogous to the modern eastern Asian Notophyllous Broad-leaved Evergreen forests near the transition with Paratropical Rain forests (Wolfe, 1978, 1992; refer to Figure 4-5). By the beginning of the Oligocene, the climate had cooled by about 8°C MAT to become temperate (Wolfe, 1992), and the earlier evergreen forests were replaced by dominantly broad-leaved deciduous forests such as Bridge Creek. The dynamic processes of plant community change can be inferred by a comparison of these latest Eocene and early Oligocene floras.

Metasequoia was an important participant during this period of changing biotic communities. A consideration of its response to the Eocene-Oligocene transition and its role in the development of Mixed Mesophytic Forest during the earliest Oligocene leads to a comparison with various Eocene and older floras. *Metasequoia* was absent from the Eocene forests of the John Day Basin, but it is one of the dominant elements not only in the Oligocene Bridge Creek flora of this area, but also in other west coast Oligocene floras such as Lyons

(Meyer, 1973). *Metasequoia* was present at sites in western North America as early as the Late Cretaceous and Paleocene (Yang, 1999; Yang & Jin, 2000; LePage *et al.*, this volume), and it was present during the Eocene in floras such as the upland and more northerly middle Eocene Republic flora of Washington (Wehr & Schorn, 1992). During the late Eocene, it occurred in the subtropical to paratropical (MAT ∼20°C) vegetation in the Bilyeu Creek flora of coastal Oregon, the transitional temperate-subtropical (MAT ∼12 to 17°C) vegetation of moderate elevation in the Cedarville flora in northeastern California (Myers, 2003) and the upland temperate forests of the Rocky Mountains of Montana (Becker, 1969). It dispersed into the John Day Basin sometime after 38.8 Ma and before 33.6 Ma (Manchester, 2000; Smith *et al.*, 1998), most likely during the Eocene-Oligocene climatic transition 33.6 to 34 Ma. It became a widespread, dominant member in the cooler, temperate (MAT ∼10 to 12°C) vegetation of this region by the beginning of the Oligocene.

The Bridge Creek flora represents the widespread development of temperate hardwood deciduous forests in mid-latitudes of the Northern Hemisphere during the early Oligocene, and it provides important evidence about the timing and mechanism of community change and the origin of Mixed Mesophytic Forest during the Eocene-Oligocene transition. Throughout the history of its study, two fundamentally different concepts have been offered to explain the mechanisms of this change.

As discussed previously, Chaney had explained this community change as an "Arcto-Tertiary geoflora" (a temperate broad-leaved deciduous forest) that developed at high latitude during the Late Cretaceous and early Tertiary, persisted there into the Eocene, and moved southward by the beginning of the Oligocene, generally maintaining a stable community structure that underwent little change in floristic composition (Chaney, 1938, 1940, 1947, 1948a). This Arcto-Tertiary model was largely discredited as a valid mechanism for community change however, based on theoretical grounds with respect to the interactions between population genetics, physiological tolerances of individual species, and changing environments. In this regard, Mason (1947) argued that plant communities and their components were dynamically changeable through time, and that these communities could not maintain the type of temporal and spatial stasis in composition envisioned by the geofloral model. Later, additional evidence against the geofloral model showed that Eocene floras from Alaska were subtropical to paratropical and lacked the temperate physiognomy and floristic composition assumed by the geofloral model (Wolfe, 1972, 1977). This interpretation of Alaskan paleofloras is complicated however, by their occurrence on accreted terranes that moved northward at some time during the Tertiary, and some of these terranes may have been at more southerly latitudes at the time their subtropical floras were deposited. However, other evidence does in fact indicate that high-latitude middle Eocene fossil forests of Arctic Canada represented a temperate forest containing a large component of broad-leaved deciduous genera (Basinger, 1991).

A more plausible hypothesis for Eocene-Oligocene community change maintains that the components of plant communities responded to the climate change not *en masse*, but rather by the responses of individual species within the communities (Mason, 1947; Wolfe, 1972). The Mixed Mesophytic Forests of the early Oligocene, as exemplified by the Bridge Creek flora, developed by the congregation of taxa that originated in older Eocene forests of different types. Forest composition changed dynamically during this time as individual taxa had one of several responses to changing climate: 1) extinction or extirpation; 2) pre-adaptation or evolution in place; 3) dispersal from higher elevations; or 4) dispersal from higher latitudes. New plant communities of unique floristic composition developed from these dynamic mechanisms. An examination of latest Eocene lowland floras provides evidence for points 1 and 2, whereas latest Eocene floras of high elevation, or middle Eocene floras of the high latitudes, provide evidence for points 3 and 4. Examples of these follow.

Extinction or extirpation eliminated many genera that participated in the late Eocene lowland floras of the Pacific Northwest by the early Oligocene. Others, such as *Craigia* W.W. Smith *et* W.E. Evans, *Cruciptera* Manchester, *Litseaphyllum* Wolfe and *Palaeophytocrene* Reid *et* Chandler, were present in late Eocene floras of the region and survived by pre-adaptation or rapid evolution to become members of the Mixed Mesophytic Forest community represented by Bridge Creek. *Metasequoia* is absent from most late Eocene coastal lowland floras of western Oregon, such as Goshen (Chaney & Sanborn, 1933; dated as 34.85 to 33.7 Ma according to Myers *et al.*, 2002) and Comstock (Sanborn, 1937), although it is present in the nearby Bilyeu Creek and Scio floras (both undated but probably correlative to Goshen according to Wolfe, 1992). Bilyeu Creek and Scio (Sanborn, 1947) possibly represent the interval during the Eocene-Oligocene climatic cooling event, at which time *Metasequoia* was entering the lowland forests of this region.

Evidence for the flora and vegetation of the late Eocene uplands comes from paleofloras such as the Florissant flora of Colorado (MacGinitie, 1953; Manchester, 2001; Meyer, 2003), the Beaverhead basin floras of southwestern Montana (Becker, 1969), and the Badger's Nose and Steamboat Canyon assemblages of the Cedarville flora of northeastern California (Myers, 2003). The Florissant flora is dated as 34.1 Ma, and various paleobotanical estimates indicate a high paleoelevation of 1900 to 4100 meters (summarized in Meyer, 2001) for this area in the southern Rocky Mountains. Florissant represents dominantly deciduous vegetation that included significant coniferous and broad-leaved evergreen components. Rainfall was less and more seasonal than at Bridge Creek, and MAT was about 12 to 14°C, although various estimates range from <11 to >18°C (summarized in Meyer, 2001). The flora indicates that many of the Bridge Creek genera had also occupied the warm temperate forests of the Eocene uplands in the continental interior. Examples include *Torreya* Arnott, *Sequoia*, *Mahonia* Nuttall, *Asterocarpinus* Manchester *et* Crane, *Ribes* L., *Amelanchier* Medik., *Crataegus* L., *Rosa* L., *Rubus* L. and *Acer* L., among others, but *Metasequoia* does not occur at Florissant. The Beaverhead floras are similar in age to Florissant and are also upland, and among the genera shared with Bridge Creek are *Metasequoia*, *Sequoia*, *Betula* L. or *Alnus*, *Paracarpinus* Manchester *et* Crane, *Rosa*, *Cercidiphyllum*, *Acer* and *Mahonia*. The Cedarville flora, probably of mid-elevation, is approximately 35 Ma and has an estimated MAT of 12.5 to 17°C (Myers, 2003). Cedarville shares such typical genera as *Metasequoia*, *Plafkeria* Wolfe, *Parrotia* Meyer and *Amelanchier* with Bridge Creek, but it also contains subtropical genera shared with the coeval low elevation Goshen-type floras mentioned above (Myers, 2003). These various late Eocene floras of the uplands represent diverse locations, elevations, and plant communities, but they provide a broad indication about the temperate genera that probably dispersed from upland regions during the climatic cooling to become members of the developing Mixed Mesophytic Forest of Oligocene low- to mid-elevation sites such as Bridge Creek. They also document the presence of *Metasequoia* at some locations in the mid-latitude uplands of the late Eocene.

Evidence from Napartulik on Axel Heiberg Island in high-latitudes of the Canadian Arctic indicates that coniferous forests with diverse broad-leaved deciduous elements occupied this region during the middle Eocene. Paleolatitude at this site is thought to have been near the present latitude of 80°N (Irving & Wynne, 1991). Various lithologically-controlled assemblages of the Buchanan Lake Formation show differences in the floristic composition that represent the local vegetational mosaic (Basinger, 1991; Greenwood & Basinger, 1994), including an *in situ* forest of *Metasequoia* stumps and leaf litter assemblages that are dominated by *Metasequoia*. The age of this formation is considered to be middle or possibly late Eocene based on palynology (McIntyre, 1991) and fossil brontotheres (Eberle & Storer, 1999), but radiometric dates are not available. The flora contains deciduous broad-leaved plants such as *Alnus*, *Betula*, *Cercidiphyllum*, *Carya* Nuttall, *Platanus* and *Quercus*, and conifers including *Metasequoia*, *Glyptostrobus* Endlicher, *Larix* Miller, *Picea* A. Dietrich, *Pinus* L., *Tsuga*, *Abies* Miller and *Pseudolarix* Gordon (Basinger, 1991; LePage, 2001, 2003; LePage & Basinger 1991, 1995). Basinger *et al.* (1994) used the NLR method to infer a MAT of 12–15°C, a mean warm month temperature >25°C, and a mean cold month temperature of 0–4°C. The diversity of conifers, however, and particularly the abundance of *Picea*, suggests instead a setting within or marginal to Mixed Coniferous forest, with a mean warm month temperature of less than 20°C and a MAT of less than 13°C based on the modern distribution for this vegetation (refer to Figure 4-5 for thermal distribution). This is not inconsistent with the MAT estimate of 9.3°C that Greenwood & Wing

(1995) derived from physiognomic criteria. The Axel Heiberg forest is thought to have grown under conditions of long winter darkness, but with mild winter temperatures lacking prolonged frost (Basinger, 1991), which would represent an environment unlike any that exists today. Thus, inference of paleoclimatic conditions based on the distribution of modern vegetation and flora would not apply well to high latitude areas where winter darkness, besides temperature, imposed limitations favoring deciduous plants. The floristic composition of this high latitude forest suggests that it might have provided a source area for particular genera that dispersed southward during the Eocene-Oligocene climatic cooling, although most of these genera were already present in the upland floras of lower latitudes during the late Eocene. It is emphasized that any southward dispersal would have involved individual lineages and not entire communities as hypothesized by the Arcto-Tertiary geofloral concept.

Although the latest Eocene was warm, an earlier cool interval during the late part of the middle Eocene in the Pacific Northwest is evidenced by floras such as the White Cap Knoll flora, occurring lower in the John Day Formation than the Bridge Creek flora and dated about 38.8 Ma (Manchester, 2000; Myers, 2003). This flora is dominated by typically temperate genera and shares many genera with Bridge Creek including *Mahonia*, *Platanus*, *Ulmus* L., *Quercus*, *Alnus*, *Palaeocarya* Saporta, *Cruciptera*, *Craigia*, *Hydrangea* L., *Rosa* and *Acer*, among others (Manchester, 2000). Notable, however, is the absence of *Metasequoia* or any other conifer. The White Cap Knoll flora indicates that temperate broad-leaved deciduous vegetation occupied this region during a cool interval that preceded the cooling of the Eocene-Oligocene transition by about 5 Ma, but the flora does not clearly suggest Mixed Mesophytic Forest, particularly by the total lack of conifers and the low diversity of broad-leaved species. Presumably, many of the temperate genera of this low to mid-elevation flora retreated to higher elevations during the intervening warm interval that preceded the Eocene-Oligocene cooling. This earlier cooling event evidently produced distributional shifts in vegetation and floristic composition comparable to those of the Eocene-Oligocene transition.

Wolfe (1972, 1977) presented a theory on the origins of the Mixed Mesophytic Forest, based on its recognition by floristic composition and vegetational physiognomy. He considered that the Mixed Mesophytic lineages originated in part from the subtropical lowland forests of the Eocene, and in part from the temperate upland forests of the Eocene, and that the modern floristic and vegetational character of the Mixed Mesophytic Forest developed primarily during the early and middle Miocene from the relatively impoverished vegetation of early Oligocene floras such as Bridge Creek. However, Wolfe (1981) considered the Bridge Creek flora to be Mixed Mesophytic Forest, although he noted that the reduced broad-leaved evergreen component of the flora was anomalous and that the diversity was depauperate relative to the modern Mixed Mesophytic Forests

(Wolfe, 1972). Meyer & Manchester (1997) pointed out that the Bridge Creek flora contains greater diversity than previously thought, and considered that it represents Mixed Mesophytic Forest near the transition to Mixed Northern Hardwood forest, but with less diversity than the modern Mixed Mesophytic Forest of Asia. Indeed, the Bridge Creek flora probably represents the rudimentary development of Mixed Mesophytic Forest, although the regional flora apparently had not fully recovered its potential floristic diversity following the impoverishment brought about by the major climatic cooling of the Eocene-Oligocene transition. As diversity increased during the early Miocene, middle latitude forests developed a greater similarity to Mixed Mesophytic Forest both floristically and physiognomically (Wolfe, 1972).

The Bridge Creek flora includes the oldest verifiable records of *Keteleeria* Carrière, *Fagus* L., *Pterocarya* Kunth and *Ostrya* Scopoli, all of which are components of the modern Mixed Mesophytic Forest in the area in which *M. glyptostroboides* occurs (Wang, 1961; Wang, 1999). The early Oligocene flora represents the earliest congregation of taxa, assembled from older dissimilar vegetation and communities, to form a forest recognizable as Mixed Mesophytic Forest, although not yet as diverse as the modern forest. This evidently was a time of radiation of many temperate (∼microthermal) taxa (Wolfe, 1987), and the majority of the genera found in the Bridge Creek flora continued their radiation to become even more widespread and diverse in the Northern Hemisphere by the early Miocene. By the early Miocene, the Mixed Mesophytic Forest was enriched by evolutionary radiation, developing diversity within many of those families that dominate this forest in eastern Asia today. Early and early-middle Miocene fossil floras such as Clarkia (Smiley & Rember, 1985), Collawash (Wolfe, 1981) and others from the Pacific Northwest (Wolfe, 1969) document a highly diverse Mixed Mesophytic Forest, which persisted in this region until increasing summer dryness and cooler summer temperatures by the late-middle Miocene to late Miocene no longer supported this type of forest (Wolfe, 1977, 1981), and *Metasequoia* was extirpated from the region. Floras similar to parts of the Mixed Mesophytic Forest existed in Alaska during the early Miocene, and although many of these genera or even species were shared with middle latitude floras of both North America and Asia, many others were restricted to only one of these continents (Wolfe, 1972). Much of the similarity was lost during the later Neogene as climate cooled in Alaska and became seasonally dry in western North America. The trans-Pacific early Miocene distribution through Alaska probably explains some of the similarity of the Tertiary western American floras to the modern Mixed Mesophytic Forest of Asia, but as Wolfe (1972) noted, the Mixed Mesophytic Forest has had a complex history, with various taxa diversifying at different times and in different regions, and it probably developed independently in several areas from the relatively depauperate vegetation of the Oligocene.

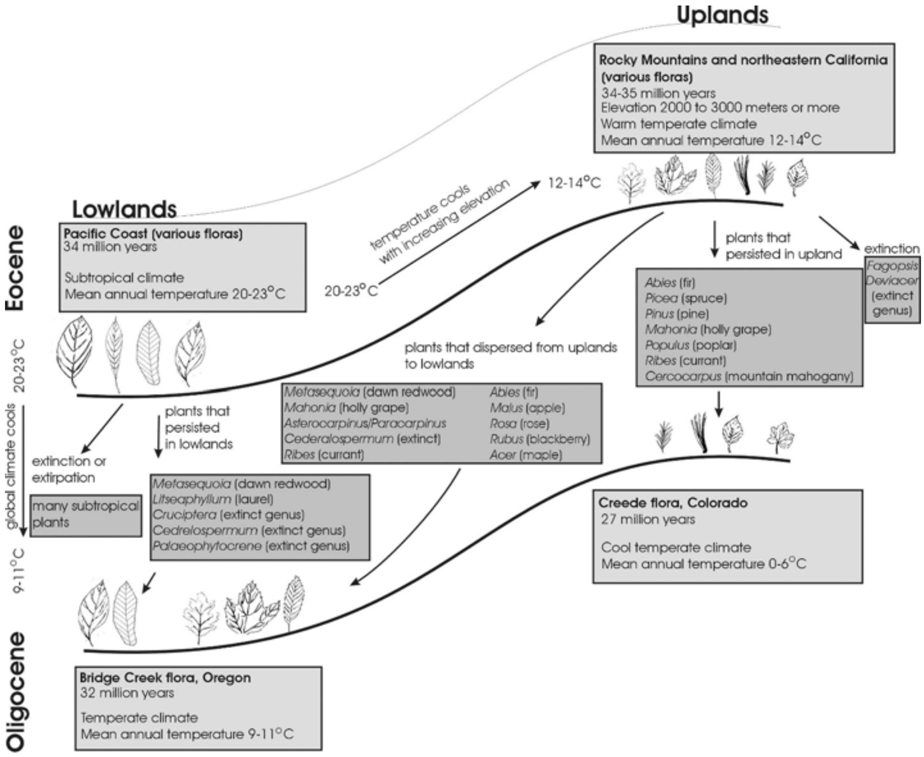

Figure 4-7. This model illustrates the dynamics of changing communities during the climatic cooling of the Eocene-Oligocene transition. Upper profile shows an idealized altitudinal transect for the late Eocene, and the lower profile does the same for the Oligocene. The Oligocene temperate forests of the lowlands, such as Bridge Creek, originated by dispersal of genera from temperate late Eocene floras of the uplands (or possibly also higher latitudes, not illustrated here), or from taxa that had participated in the late Eocene subtropical or paratropical forests of the lowlands and persisted in this area during development of the temperate forest because of pre-adaptation or rapid evolution to tolerate cooler conditions. *Metasequoia* is known to have occurred in late Eocene upland (mid-elevation) floras such as the Cedarville and Beaverhead floras, and it is also indicated here as persisting in the lowland because it occurs in the Scio and Bilyeu Creek floras, although it should be noted that it is lacking in most other late Eocene lowland floras of the Pacific coast. Diagram modified slightly from Meyer, 2003, courtesy of Smithsonian Books.

A model for the dynamics of community change during the Eocene-Oligocene transition is illustrated by Figure 4-7. This idealized model shows some of the probable multiple sources for various genera that became a part of the Bridge Creek community. Some of the genera, including *Metasequoia*, apparently had sufficiently widespread distribution by the latest Eocene to have been derived from more than one potential source, either from higher elevation or higher latitude, or by persistence in the changing environments and forests of the lowlands. *Metasequoia* had been a participant in various late Eocene forests that included, for example, the mid-elevation Badger's Nose assemblage of the Cedarville flora (Myers, 2003) about 300 km south of the nearest Bridge Creek flora localities, and the lowland Bilyeu Creek and Scio floras about 180 km west of the Bridge Creek flora. The Eocene floras of central Oregon near the Bridge Creek sites did not, however, contain *Metasequoia*, suggesting that the genus dispersed instead from nearby regions. The dispersal of *Metasequoia* into the floras of central Oregon, such as Bridge Creek, apparently post-dated 38.8 Ma.

7. CONCLUSIONS

The description of *Metasequoia* from the fossil record of Japan and the subsequent discovery of living trees in central China during the 1940s had a profound effect on American paleobotany in terms of understanding both the floristic composition of fossil floras and the mechanisms that determined the origin and development of Tertiary forests in western North America. The Bridge Creek flora illustrates many aspects of this story, from the early description of fossils as *Sequoia* and the misleading interpretations to which that led, to the discovery of *M. glyptostroboides* and the influence this had on R.W. Chaney's reinterpretation of the Tertiary forests of western North America, to more recent models that infer a dynamic origin of Mixed Mesophytic Forest during the early Oligocene.

The evolution of forest types through time represents a dynamic continuum in which individual lineages are in a constant state of flux, and the history of any vegetation type, such as Mixed Mesophytic Forest, is complex (Wolfe, 1972, 1977; Mason 1947). Periods of significant climate change, such as the one that preceded the Bridge Creek flora, provide the impetus for rapid change of forest composition, and it is during such periods that forest communities are most affected. In this respect, the cooling of the Eocene-Oligocene transition was a major stimulus in the early origin of Mixed Mesophytic Forest, and the Bridge Creek flora represents an important stage in the development of this forest type. The various components of this early Oligocene forest had their origins in the subtropical to paratropical Eocene lowland forests and/or the temperate Eocene upland or high latitude forests. *Metasequoia* was a dominant participant in this developing Mixed Mesophytic Forest of the early Oligocene. The fossil evidence suggests that it became a member of subtropical lowland forests in the Pacific Northwest immediately preceding or during this climate change, and that it participated in Eocene temperate forests at higher latitude or elevation. Subsequent to the Oligocene, the fossil record from the Pacific Northwest demonstrates that the Mixed Mesophytic Forest became further enriched through evolutionary radiation (e.g., *Acer* and genera of the Rosaceae) and by the assimilation of new genera (e.g., members of the Ericaceae), although a few other genera (e.g., *Asterocarpinus*, *Cruciptera* and *Florissantia* Knowlton) were lost to extinction. Although the modern Mixed Mesophytic Forest is not identical to the Bridge Creek flora, it remains as the closest modern derivative, both in terms of floristics and physiognomy. Today, *M. glyptostroboides* persists as an endemic relict in this forest.

Currently, *M. glyptostroboides* is represented by only 5770 trees that are thought to be naturally occurring. Evidence also suggests, however, that much of the original *M. glyptostroboides* forest was lost following human occupation 250 years ago. The few remaining stands of natural *M. glyptostroboides* serve as an icon not only for the preservation of an endangered "living fossil" genus, but moreover for the preservation of the Mixed Mesophytic Forest as an *entire community* that forms the world's most diverse temperate forest ecosystem (Langlois, this volume). The conservation of this forest type is important not only for maintaining the modern biotic diversity of the planet, but also for providing an important reference point for understanding Tertiary fossil floras and the evidence they provide about the ecology and evolution of forest communities through time.

8. ACKNOWLEDGEMENTS

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Chapter 5

Gunther's Travels: The Odyssey of *Metasequoia* Seeds from the 1920s?

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Abstract: The story of the establishment of the fossil genus *Metasequoia* Miki in 1941 by the Japanese paleobotanist S. Miki and the discovery and classification of the living *Metasequoia glyptostroboides* Hu *et* Cheng (Dawn Redwood) in 1946–1948 by Professors H. H. Hu and W.C. Cheng are well known. In addition, the efforts of Elmer D. Merrill of the Arnold Arboretum of Harvard University and paleontologist Ralph Chaney of the University of California, Berkeley to collect and disperse *M. glyptostroboides* seeds throughout the world have been carefully chronicled. But what is not well-known is the story of how Wilhelm Gunther (1893–1983), a German national who lived and worked in China between 1914 and 1941, acquired seeds in the late 1920s that decades later would be identified as those of *M. glyptostroboides*. Drawing from historical and contemporary photographs as well as interviews with Gunther's daughters, this essay unravels the odyssey of these *M. glyptostroboides* seeds that possibly predate the discovery of the native population in China.

Key words: Blithewold; China; Hankou; Hubei Province; redwoods; Rhode Island; Shui-sha-ba Valley; Warwick Neck; Yangtze River.

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1. INTRODUCTION

The story of the establishment of the fossil genus *Metasequoia* Miki in 1941 by the Japanese paleobotanist S. Miki (Miki, 1941) and the discovery and classification of the living *Metasequoia glyptostroboides* Hu *et* Cheng (Dawn redwood) in 1946–1948 by Professors H.H. Hu and W.C. Cheng are well-known (Hu, 1948; Hu & Cheng, 1948; Hsueh, 1985). In addition, the efforts of Elmer D. Merrill of the Arnold Arboretum of Harvard University and paleontologist Ralph Chaney of the University of California, Berkeley to collect and disperse *M. glyptostroboides* seeds have been carefully chronicled (Chaney 1948; Merrill, 1948). But what is not well-known is the story of how Wilhelm Gunther (1893–1983), a German national who lived and worked in China between 1914 and 1941, acquired seeds in the late 1920s that decades later would be identified as those of *M. glyptostroboides* (Richardson, 1995). Drawing from family photographs as well as interviews with Gunther's daughters, this paper will unravel the odyssey of these *M. glyptostroboides* seeds.

2. GUNTHER IN CHINA

In April 1914, Wilhelm Gunther began working in Shanghai for Melchers and Company, a large German import and export company. When World War I broke out that summer, the 3,000 Germans who worked in China were ordered to defend Qingdao, a port city on east China's Shangdong Peninsula that had been a German concession since 1897. Japan seized control of Qingdao in 1914, and most of the 3,000 Germans who had been sent there to fight the Japanese, including Gunther, were taken as prisoners of war and shipped to Kurume, an island off the southern tip of Japan. They were held at Kurume until 1919, the year after World War I ended. Upon Gunther's release from Kurume, he returned to Shanghai and resumed working for Melchers.

In 1924, Melchers awarded Gunther a ten-month vacation—one month for each year he had worked for Melchers, including his almost five years as a German POW. Gunther used this opportunity to travel to California where he visited Yosemite National Park and saw trees of *Sequoia giganteum* (Lindley) J. Buchholz (Giant redwood). He then traveled by train across the North American continent to Staten Island, New York to visit relatives. During his stay in Staten Island, he met his future wife's family. Gunther then continued on to Germany, traveling aboard a ship where his future wife, Emilie Marcella Stirn, was also a passenger. During their trip across the Atlantic Ocean, the couple fell in love. After landing in Bremerhaven, Wilhelm purchased a diamond engagement ring and proposed to Marcella. Their courtship continued for several months. In the late summer of 1925, he went back to China via the Trans-Siberian Railroad. He returned to New York in the spring of 1926, and the couple was married in a double-wedding ceremony on May 11, 1926. Shortly after their marriage, the newlyweds settled in China, first living in Shanghai and later in Tianjing. A daughter, Dagmar, was born in 1931. A second daughter, Mignon, was born in 1934.

Not long after arriving in Shanghai, Marcella became ill and left China to go to a sanatorium in Davos, Switzerland, where she eventually regained her health. In late 1927, during his wife's absence, Gunther traveled by houseboat along the Yangtze River to Hankou where he gathered seeds from a tree that fascinated him and that some fifty years later would be identified half a world away in Rhode Island as those of the *M. glyptostroboides*. Gunther's daughters have speculated that their father came across *M. glyptostroboides* trees during his trip to Hankou and that these trees probably reminded him of the Giant redwood trees he had seen when visiting Yosemite National Park in 1924 (Mignon Gunther-Kolb, personal communication, April 20, 2002; Dagmar Gunther-Stirn, personal communication, April 8, 2002, May 1, 2002). After all, it is plausible that *M. glyptostroboides* trees grew in the immediate vicinity of Hankou in the late 1920s. Still, why Gunther gathered these particular seeds from an unknown tree at this time remains a mystery. Family photographs corroborate that Gunther traveled by houseboat along the Yangtze River to Hankou in 1927, but, unfortunately, Gunther's diaries, journals, and letters, which might have provided more precise information about how and why he gathered these seeds, were destroyed before he died.

What we do know is that the survival of these seeds during the political and social mayhem of the next twenty-five years is truly astounding. By the late 1920s, civil war had broken out in China. Adding to this turmoil, Japan seized Manchuria in 1931 and by mid 1937 a full-scale Sino-Japanese war had erupted. At this point, Marcella and her two young daughters left China and headed to Germany to live. They traveled by ship via the South China Sea to Singapore, India and the Suez Canal, eventually making their way to Germany. However, Marcella was displeased with the Nazi education that her daughters received in her husband's native country, and, consequently, the family spent part of the next two years in Switzerland where the children were educated.

With the outbreak of World War II in Europe in September 1939, Gunther's wife and daughters returned to the United States to live with relatives in New York. Gunther headed back to China, via the Trans Siberian Railroad, arriving there in January 1940. He made a brief trip to the United States in the spring of 1940 and then returned to Tianjing in the summer of

1940 to take care of various business affairs and pack up their household belongings for shipment to the United States. Among the goods shipped back to the United States was the packet of seeds that he had collected in 1927. A year later, in June 1941, Gunther was reunited with his wife and daughters in New York.

3. GUNTHER IN AMERICA

Over the next few years, the family made several moves throughout the northeastern United States. Following the official entry of the United States into World War II in December 1941, Gunther, like many other German-Americans and German aliens, experienced significant prejudice and discrimination. Indeed, at one time United States officials suspected him of knowing an important Nazi simply because he received a postcard from a German friend still living in China. Nevertheless, he was recruited to do important work in the precious metal industry in Attleboro, Massachusetts (Krammer, 1997). In 1948, three years after World War II ended, the family made their last move and settled permanently in Warwick Neck, Rhode Island. By this time, Gunther had acquired J.L. Anthony and Company, a prominent jewelry manufacturing business in Rhode Island.

Amazingly, the seeds acquired by Gunther in 1927 survived war in China as well as various family moves throughout the northeastern United States during the 1940s. In fact, both daughters clearly remember that when they settled in Warwick Neck, Rhode Island in 1948, the packet of seeds from China was placed in the drawer of a small antique desk at their home (Mignon Gunther-Kolb, personal communication, April 20, 2002; Dagmar Gunther-Stirn, personal communication, April 8, 2002, May 1, 2002).

Around 1950 or 1951, Gunther decided to take the seeds to the gardener at Blithewold, then a privately owned mansion dating from the early 1900s in Bristol, Rhode Island that was well-known for its Oriental gardens, to see if the seeds could be germinated (www.blithewold.org). Two of them did germinate. One seedling was planted at the Gunther home in Warwick Neck; the other was planted at Blithewold. Finally, Gunther had a chance to see the beautiful tree that he had so admired in a small village along the Yangtze River many years earlier. Why Gunther picked this particular time to see if the seeds could be germinated is unclear. Perhaps he had heard of the recent discovery of the "living fossil" tree and the efforts of the nearby Arnold Arboretum to collect and disperse *M. glyptostroboides* seeds for these events were the topic of a number of newspaper articles (Pittsburgh Press, 1948; Silverman, 1948).

4. GUNTHER'S *METASEQUOIA*

Both daughters have vivid memories of the day in 1950 or 1951 when their father proudly brought the *M. glyptostroboides* seedling to their home and planted it not far from their barn in their backyard where it still stands today (Mignon Gunther-Kolb, personal communication, April 20, 2002; Dagmar Gunther-Stirn, personal communication, April 8, 2002, May 1, 2002). With a circumference of 8 feet 3 inches (2.5 m) and a diameter of 2 feet 8 inches (0.81 m), the tree is about the same size as those planted at the Arnold Arboretum in the late 1940s and early 1950s (Figures 5-1 and 5-2; H. Yang, unpublished). A two-foot high (0.61 m) *M. glyptostroboides* seedling is growing in the garden not far from the original tree.

Figure 5-1. Mignon Gunther-Kolb and the author standing next to the *Metasequoia glyptostroboides* planted at the Gunther home in Warwick Neck, Rhode Island, USA.

Figure 5-2. Metasequoia glyptostroboides growing at the Gunther home in Warwick Neck, Rhode Island from one of the two seeds that germinated from Gunther's seeds that he collected in Hankou, China in 1927.

The *M. glyptostroboides* tree at Blithewold is larger. It has a circumference of 12 feet 9 inches (3.9 m) and a diameter of 4 feet (1.2 m). The larger size of the Blithewold *M. glyptostroboides* is most likely due to the fact that it was planted in an open field rather than in a crowded backyard. It is planted about 50 yards (46 m) from Blithewold's 100-foot (30.5 m) tall Giant redwood tree, the largest of its kind east of the Rocky Mountains. In fact, the *M. glyptostroboides* at Blithewold is about the same height as the Giant redwood, which was planted in 1911 and has grown at the rate of approximately one-foot (0.3 m) per year. Unfortunately, the horticultural records of Blithewold are incomplete, especially for the period prior to 1976 when it was a private residence. The mostly unprocessed Blithewold archives, including some family photographs and albums, which might provide additional information about the origins of the Blithewold *M. glyptostroboides* are closed to the public.

Since *M. glyptostroboides* seeds have a relatively low germination rate of 6–8% as compared to other conifers (Vann *et al.*, 2003), it would be helpful if we knew the number of seeds that were given to the gardener at Blithewold. Unfortunately, we do not have the answer to this question, nor can we be sure that all of the seeds that were in the original packet were those of *Metasequoi*a.

Not until after Dagmar Gunther-Stirn visited Yosemite National Park in 1976 did she realize that the two trees that had been planted around 1950 were, in fact,*M. glyptostroboides* trees. Until that time, the Gunther family had referred to the tree in their backyard as the "Chinese tree." Gunther-Stirn told the forest ranger at Yosemite that she had a tree like the Giant redwoods, but that it shed its needles each winter. The park ranger responded that Giant redwoods did not shed their needles and that the tree that she had described was something other than a Giant redwood. Before leaving Yosemite, Gunther-Stirn purchased a book about the trees of the national forest that included a brief description of *M. glyptostroboides*. It was only after reading this book that she realized that the "Chinese tree" at Warwick Neck was *M. glyptostroboides* (Dagmar Gunther-Stirn, personal communication, April 8, 2002, May 1, 2002).

In the spring of 2002, Professor Hong Yang and I collected leaf samples from the two Rhode Island *M. glyptostroboides* trees. We sent the samples to the Nanjing Institute of Geology and Paleontology of the Chinese Academy of Sciences where Qin Leng conducted cuticle micromorphological studies. She compared the Rhode Island samples with those from a larger data base of known *Metasequoia* cuticles, both fossil and living, and determined that the cuticle from the two Gunther trees are identical to the uneven type of cuticle that is widely spread among the *M. glyptostroboides* trees located in the Shui-sha-ba Valley in Hubei Province. Qin Leng's study, therefore, cannot confirm that Gunther's seeds came from a population that was outside of the Shui-sha-ba Valley (Qin Leng, personal communication, August, 2002). However, the possibility that the seeds came from *M. glyptostroboides* trees that may have been located near Hankou in 1927 cannot be ruled out. While further molecular work would provide additional information, it is unlikely that such information could verify the sources of the Gunter seeds (Hong Yang, personal communication, August, 2002).

For the origin of Gunther's *M. glyptostroboides* seeds to be definitively established, additional historical records must be discovered. Oral histories, such as those related by Gunther's two daughters, represent an important source of information. Moreover, family photographs have established that Gunther traveled by houseboat on the Yangtze River to Hankou in 1927, but unfortunately, trees of *M. glyptostroboides* no longer exist in Hankou and none are featured in his photographs. What is missing of course, are relevant primary source materials, such as diaries, journals, letters, or record books; and, it is primary source materials that make up the essential tools of the historian's trade. If written sources are uncovered that augment the oral histories provided by

Gunther's daughters, we could then be confident that the seeds were gathered around Hankou in 1927. Until such written materials come to light, we can only speculate on the origins and odyssey of Gunther's *M. glyptostroboides* seeds.

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PART II

Cuticle, Ultrastructure and Biomolecules

Chapter 6

Cuticle Analysis of Living and Fossil *Metasequoia*

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Abstract: The recent discovery of two distinct cuticle types, Uneven Type and Even Type, within the native population of *Metasequoia glyptostroboides* Hu *et* Cheng has prompted re-evaluation of the taxonomic utility of cuticle characters in both living and fossil *Metasequoia* Miki. The result is a comprehensive review of the existing data and methods used in the past to analyze living and fossil cuticle, as well as the impact of cuticle analyses for interpreting the evolutionary history of the genus. Previous studies on the cuticle micromorphology of living and fossil *Metasequoia* are discussed. The application of scanning electron microscopy (SEM) methodology is deemed critical for re-evaluating the results previously obtained using light microscopy (LM) techniques and allows reinterpretation of some of the cuticle characters that were either poorly understood or misinterpreted. Except for the possible presence in immature seedlings, the Even Type cuticle appears to be restricted to a tree in Paomu Village in Hunan Province, China; whereas the Uneven Type cuticle is widely distributed in the main *M. glyptostroboides* population. So far, all of the fossil materials examined for cuticle micromorphology possess the Even Type, suggesting that the Even Type cuticle is the ancestral character state for the genus. This finding bears significant

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implications for the evolution and paleogeography of this genus, as well as the conservation of this endangered species. Further research perspectives using cuticle analyses should provide us with a better understanding of the origin and distribution of these different cuticle types in both living and fossil material.

Key words: cuticle analysis; Uneven Type; Even Type; evolution; phylogeny; taxonomy.

1. INTRODUCTION

The existence of a plant cuticle membrane (*sensu* Holloway, 1982a), or more generally referred to as "cuticle", has been known for nearly two centuries. Plant cuticle is a continuous extra-cellular layer covering the outer surfaces of the aerial parts of plants, mainly leaves, fruits and non-woody stems (Stace, 1965; Holloway, 1982a; Mösle *et al.*, 1997). The structure and exact chemical composition of plant cuticle is still debatable (for structure the readers are referred to Holloway, 1982a and for chemical composition to Holloway, 1982b; Tegelaar *et al.*, 1991; Heredia, 2003) and varies largely among taxa, organs and various growth stages (Holloway, 1982a; Jeffree, 1996). However, there is consensus that plant cuticle is chemically composed of a highly resistant macromolecular material that possesses stable physical and chemical properties. These properties ensure its fundamental role as a protective barrier between the plant and its environment. The cuticle minimizes water loss and helps protect the plant against physical, chemical and biological harm. Thus, together with intercellular air spaces, lignin and the seed habit, cuticle is considered to be one of the "four great inventions of the land plants" (Corner, 1964).

Apart from its physiological functions, the taxonomic value of cuticle has been recognized by botanists and particularly paleobotanists who are forced to deal with chemically stable plant remains that have been preserved in the fossil record. There are three factors contributing to the taxonomic function of cuticle. First, the cuticle itself possesses many intrinsic characters, which may be of taxonomic value, especially when these characters are investigated using scanning electron microscopy (SEM) (Boulter, 1971). Second, as cuticle is deposited over the surface of the epidermal cell walls, an impression of the periclinal and anticlinal surfaces of the epidermal cells is preserved (Collinson *et al.*, 1998). Thus, cuticle can be used to explore a wide range of leaf epidermal characters such as the size and shape of epidermal cells, the type and arrangement of stomata, hair bases and other structures. Third, due to its stable chemical structure and composition, cuticle has a high potential to survive a wide array of biological and geological processes. Following harsh chemical treatments, the cuticle of living plants, as well as cuticle from fossil leaves that are preserved as coalified plant compressions or dispersed fossil fragments (dispersed cuticle) can be prepared as transparent membranes that are readily observable under the light microscope (LM) or SEM. It is interesting to note that although fossil cuticle might have been modified chemically to a large extent during diagenesis, the original internal and external morphological and ultrastructural features are commonly well preserved and unaltered (Collinson *et al*., 1998; Mösle *et al*., 1998). In this sense, cuticle may be considered as the "external skeleton" of plants (McElwain & Chaloner, 1996), and cuticle analysis (the study of plant cuticle, termed by Florin, 1951) can therefore be used as an important and essential paleobotanical and botanical technique for taxonomy and systematics.

Among the pioneers who effectively demonstrated the taxonomic value of cuticle, Thomas & Bancroft's (1913) achievement in separating the bennettitalians from the cycads based on cuticle observations, despite the fact that these two plant groups possess the same gross frond (leaf) morphology, can be viewed as a milestone. Since then, cuticle analysis has been widely used as a taxonomic tool for a variety of other plant groups, and has been proven to be an effective tool for discriminating between taxa and assigning isolated fossil organs to discrete plant taxa (e.g., Florin, 1958; Stace, 1965, 1966; Dilcher, 1974; Clement-Westerhof, 1984; Kerp, 1988). The last century has witnessed an exceptionally rapid accumulation of literature dealing with cuticle analysis, and because of the pioneering work of Rudolf Florin (Florin, 1931, 1938–1945, 1951, 1958) who revealed the potential value of cuticle in his taxonomic studies on conifers, cuticle analysis of the conifers has probably constituted the largest portion of the existing literature on plant cuticle studies.

Metasequoia Miki has been the subject of intensive scientific study and popular interest, mainly because of its interesting history of discovery and long fossil record. The genus was first recognized in the plant fossil record by Miki (1941) before its modern representative *Metasequoia glyptostroboides* Hu *et* Cheng was discovered growing in South-central China (Hu, 1946; Hu & Cheng, 1948). Accordingly, it has been named a "living fossil." Studies of its fossil record have indicated that representatives of the genus *Metasequoia* first appeared during the Late Cretaceous and soon became the dominant conifer of early Tertiary temperate floras of the Northern Hemisphere (Chaney, 1951; Yang & Jin, 2000; LePage *et al*., this volume; Meyer, this volume, Momohara, this volume). Because of its widespread occurrence in Tertiary floras, as well as its interesting history of discovery, considerable attention has been focused on this genus and these studies have resulted in a large number of publications dealing with aspects of both living and fossil *Metasequoia* (Fulling, 1976; Yang & Jin, 2000; Ma, 2003).

Based on a survey of this body of literature and particularly those dealing with cuticle studies, the objectives of this paper are to synthesize the observations made and reported on fossil and living *Metasequoia* cuticle. Second, the evolutionary implications of the cuticle characters identified in these existing and newly obtained observations of this genus are discussed. Finally, an up-to-date summary of our understanding of fossil and living *Metasequoia* cuticle and directions for future work are provided.

2. MATERIAL AND METHODS

It has been demonstrated that cuticle micromorphology varies among taxa, organs and growth stages. Thus, as a traditionally accepted rule for preparing leaves for cuticle analysis (Florin, 1958), only the central part of a mature leaf blade is used for cuticle preparation. In addition, the leafy shoots of *Metasequoia* have been reported to show a wide range of growth variation, which places restrictions and limitations on the material. According to Stockey *et al.* (2001), three kinds of leafy shoots are reported from both living and fossil *Metasequoia*: (1) compound shoots consisting of two orders of branching (A—ultimate order branches with short leaves and short internodes and B—penultimate order branches with large leaves and long internodes); (2) medium sized simple shoots with large leaves, but with short internodes; and (3) small simple shoots with short leaves and short internodes, which are morphologically similar to the ultimate order branch of the first kind. Various terms were applied by different authors to describe these variations seen in the leafy shoots, including "long shoot" and "short shoot" (Chaney, 1951; Florin, 1952; Li, 1964; Chandrasekharam, 1974), "persistent shoot" and "deciduous shoot" (Christophel, 1976), and "Type I branchlet" and "Type II branchlet" (Liu *et al.*, 1999). In this paper the terms used by Stockey *et al.* (2001) are adopted because they more precisely describe the complicated leafy shoots of fossil and living *Metasequoia*. For the sake of consistency, only the middle portion of the leaves from the middle part of the mature determinate, ultimate and unbranched shoots, including the ultimate order branches of the compound and simple shoots, which have closely spaced leaves and short internodes are suggested to be used for cuticle analysis until it can be demonstrated that the cuticle characters of leaves from these leafy shoot variations are identical. This suggestion for material selection is applicable to both living and fossil material, so long as the fossil preservation allows.

Since cuticle analysis has been regarded as one of the most important techniques employed in paleobotanical research for more than a century, the methods applied to cuticle analysis for both living and fossil material have been standardized. For brief reviews of these methods, the readers are referred to Alvin & Boulter (1974), Dilcher (1974), Kerp (1989) and Upchurch (1989). For *M. glyptostroboides* cuticle, the standard chromium trioxide (CrO_3) treatment of Alvin & Boulter (1974) and Stockey & Ko (1986) was found to yield the most consistent and high quality cuticle preparations (Leng *et al.*, 2001). The middle parts of leaf blades are cut with one leaf margin intact, leaving both upper and lower cuticle attached. They are then immersed in 20% CrO_3 solution at room temperature for 96 hr or more to obtain entirely isolated clean cuticle. The cuticle is then either mounted on glass slides that can be observed under LM or washed thoroughly in distilled water and mounted on SEM stubs for observation. External (outer) and internal (inner) surfaces of both the adaxial (upper) and abaxial (lower) cuticle of the leaf should then be observed.

As far as fossil *Metasequoia* cuticle is concerned the methods become more complicated. This is mainly due to the thin cuticle seen in both fossil and living *Metasequoia* leaves. Compared with most other conifers, which are generally evergreen and possess thick cuticle, the deciduous *Metasequoia* leaves possess thin, flimsy cuticle; as a result, fossil cuticle, particularly from the abaxial surface of the leaf, are fragile and difficult to prepare. Extreme care is required during the cuticle preparation process. Based on personal experience, room temperature Schulze solution and hypochlorite solution (Dilcher, 1974; Huggins, 1985) are applicable to the cuticle preparation of fossil *Metasequoia* leaves, as long as the concentration of the solution matches the quality of the preservation. The final concentration used however, must be determined through experimentation.

Although the taxonomic and systematic usefulness of cuticle characters revealed under LM has been long demonstrated (Florin, 1931, 1938–1945, 1951, 1958; Stace, 1965; Dilcher, 1974), the results obtained using SEM for cuticle analysis far outweigh the results obtained using LM. The higher resolution and three dimensional SEM images can not only disclose finer details of the cuticle characters, but also reveal a set of completely new features that are useful in the identification and classification of plants (Boulter, 1971; Alvin & Boulter, 1974; Stockey & Atkinson, 1993; Stockey & Frevel, 1997; Leng *et al.*, 2001). Accordingly, features that could not be observed clearly or were misinterpreted under LM can now be clarified and corrected with SEM (Leng *et al.*, 2001). Thus SEM, rather than the conventional LM, is strongly recommended for the observation of cuticle characters and is the technique of choice in this review.

3. CUTICLE OF LIVING *METASEQUOIA GLYPTOSTROBOIDES*

Along with other morphological features of *M. glyptostroboides*, the general cuticle characters were investigated with LM soon after this living species was discovered in China (Sterling, 1949; Miki & Hikita, 1951; Sze, 1951a, 1951b). Subsequent reports on *M. glyptostroboides* cuticle continued to be published, but these reports were commonly scattered throughout the literature and in many cases *M. glyptostroboides* cuticle was used as reference material for comparative purposes only (Sveshnikova, 1963, 1975a, 1975b; Huggins, 1985; Liu *et al.*, 1999). Because of the limited resolution of LM, the cuticle characters of *M. glyptostroboides* indicated that although cuticle could be used to distinguish between *M. glyptostroboides* and other taxa of the taxodioid clade (e.g., *Sequoia* Endlicher, *Taxodium* Richard and *Glyptostrobus* Endlicher) (Florin, 1951), it has limited taxonomic usage at the intra-generic level. When SEM was introduced, the cuticle characters of *M. glyptostroboides* were observed, but in a very preliminary fashion (Boulter, 1971; Alvin & Boulter, 1974; Chaturvedi, 1994, 1998).

Among the botanists who worked on cuticle micromorphology, there is an agreement that only after the cuticle characters of the living representatives have been comprehensively investigated can fossil cuticle yield meaningful interpretations (Florin, 1931; Boulter, 1971). With this in mind, a comprehensive cuticle analysis using SEM was conducted recently on *M. glyptostroboides* trees growing in its native habitat in South-central China (Leng *et al.*, 2001). The SEM observations on fully-grown mature trees from all eight groves native in Hubei Province, Hunan Province, and Chongqing Municipality Directly Under the Central Government have revealed many fine cuticle characters that are of considerable taxonomic and evolutionary value. While the cuticle characters seen in the native trees of *M. glyptostroboides* demonstrate a high degree of uniformity within these eight groves, a unique tree living in isolation in Paomu Village, a remote village near Luota Town, Hunan Province, displays cuticle characters that differ considerably from all other living trees that were sampled from the living population. The most striking difference between these two kinds of cuticle is whether the periclinal walls of the abaxial cuticle are "*Uneven*" as is the case with the main population or "*Even*" as is the case with the Paomu Tree. These two cuticle types were tentatively termed "Uneven Type" and "Even Type", and the differences are summarized in Table 6-1 and further illustrated in Figures 6-1, 6-2 and 6-3.

An extensive literature survey of the various cuticle analyses conducted on *M. glyptostroboides* has yielded interesting results. Besides those whose cuticle types are unrecognizable due to the poor quality of LM illustrations (e.g., Sze, 1951a, 1951b), the majority of reports on *M. glyptostroboides* cuticle preceding Leng *et al.* (2001) have shown Uneven or Uneven-like types (e.g., Figure 4-d in Florin, 1951; Plate II, Figures 2 and 3 in Sveshnikova, 1963; Plate I, Figure 8 in Sveshnikova, 1975a; Plate III, Figure 5 in Sveshnikova, 1975b; Plate 7, Figures 3 and 4 in Huggins, 1985). The exceptions to these results include reports by Sterling (1949), Miki & Hikita (1951), Boulter (1971) and Chaturvedi (1994, 1998) and are discussed below.

Table 6-1. Differences between Uneven and Even Types of *Metasequoia glyptostroboides* leaf cuticle observed under SEM (only abaxial cuticle, after Leng *et al.*, 2001).

Internal surface *Non-Stomatal Zone*	Uneven Type	Even Type
Epidermal Cell Shape	Elliptic	Rectangular
Anticlinal Walls	Variable in thickness*	Distinct
Periclinal Walls	Uneven	Even
Stomatal Zone		
Anticlinal Walls	Variable in thickness*	Distinct
Periclinal Walls	Uneven	Even
Subsidiary Cells	Indistinguishable from epidermal cells	Distinct
Stomata	Rectangular, no polar extension, frilled-margin lacking	Elliptical with polar extension, frill margined
External surface *Non-Stomatal Zone*	Uneven Type	Even Type
Epidermal Cells	Outline indistinct	Outline recognizable
Periclinal Walls	Uneven	Even
Stomatal Zone		
Epidermal Cells	Outline indistinct	Outline recognizable
Florin Rings	Shaped like two parallel flanges	Elliptical
Distribution	Uneven Type	Even Type
	Found in all trees sampled from the natural population, except for the Paomu Tree	Found only in a tree at Paomu Village, Hunan Province

*The anticlinal walls of the Uneven Type are of variable thickness, making the boundary of the cells indistinct to rarely more or less distinct when the thickness variation is low.

Plate III, Figure 3 in Boulter (1971) illustrates the "*M. glyptostroboides*" stomatal zone which displays an entirely different morphology from that of *M. glyptostroboides* reported elsewhere (Florin, 1951; Alvin & Boulter, 1974; Leng *et al.*, 2001). A careful comparison indicates that the distinct large "cuticle pegs" on the subsidiary and ordinary epidermal cells (described as "papillae" in Boulter, 1971, p. 222) are characteristic of *Sciadopitys verticillata* (Thunberg) Siebold *et* Zuccarini, and have not been reported from any other taxon in the Taxodiaceae. In a survey of cuticle characters among members of Taxodiaceae and Sciadopityaceae, the overall morphology of the stomatal zone illustrated in that figure resembles that of *S. verticillata* (Leng, unpublished data). In addition, the internal surface of the upper cuticle that is described as being that of "*M. glyptostroboides*", which is illustrated in Plate I, Figure 2 of Boulter (1971) is neither consistent with *M. glyptostroboides* cuticle because its coarse sculpture contrasts with the smooth fine sculptured surface of this genus that has been widely reported by others (Alvin & Boulter, 1974; Leng *et al.*, 2001). Since Boulter (1971) also used material from *S. verticillata*, it is possible that the

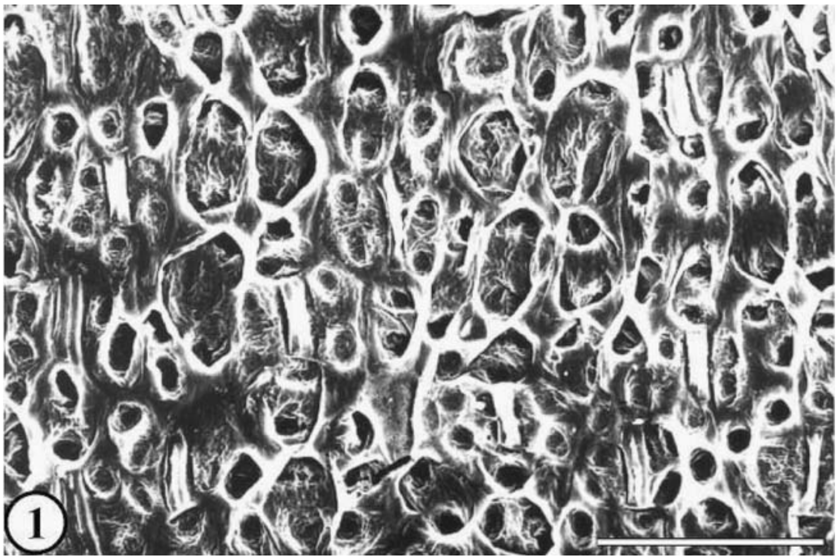

Figure 6-1. Uneven Type of cuticle characterized in a *Metasequoia glyptostroboides* leaf, showing only the stomatal zone of the internal surface of the abaxial cuticle. Scale bar = 100 μm.

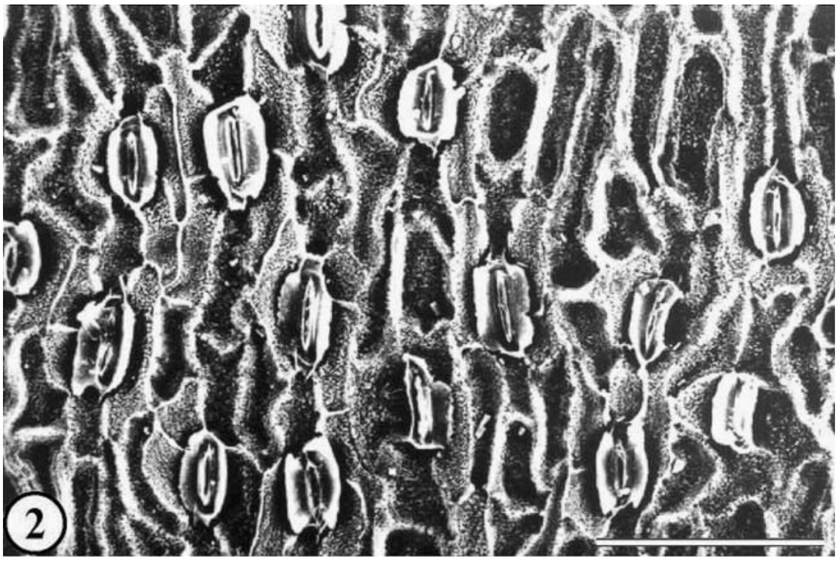

Figure 6-2. Even Type of cuticle characterized in the Paomu Tree showing only the stomatal zone of the internal surface of the abaxial cuticle. Scale bar = 100 μm.

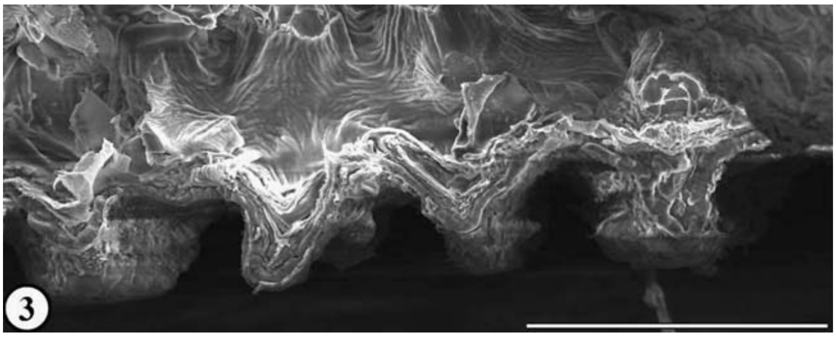

Figure 6-3. Uneven Type of cuticle characterized in a *Metasequoia glyptostroboides* leaf observed in longitudinal cross section without any chemical treatment, showing a strong outward (down) bulging (unevenness) of the cuticle membrane. Note that although it is bulging strongly, the cuticle membrane itself remains almost the same thickness. Scale bar = 30 μm.

"*M. glyptostroboides*" cuticle shown in Plate I, Figure 2 and Plate III, Figure 3 were misidentified; the latter possibly from *S. verticillata* while the former remains unknown.

The same may be said for "*M. glyptostroboides*" cuticle shown in the Figure 4 of Chaturvedi (1994) and Figures 3 and 9 of Chaturvedi (1998). All descriptions were based on LM observations from the same sample. The overall morphology of this cuticle fragment, particularly that of the stomata, is largely different from that of *M. glyptostroboides*, and thus the sample yielding the cuticle might also be from another conifer but not *M. glyptostroboides*. Interestingly, the outer leaf surface of *M. glyptostroboides* observed directly under SEM without any chemical treatments shown in those two papers (Figure 15 in Chaturvedi, 1994 and Figure 1 in Chaturvedi, 1998) are identical to the Uneven Type observed by Leng *et al.* (2001), illustrating strong unevenness of the periclinal walls.

Given that there is evidence indicating that the cuticle described in Boulter (1971) and Chaturvedi (1994, 1998) (except for Figure 15, 1994 and Figure 1, 1998) can be dismissed as being that of *M. glyptostroboides*, they will no longer be considered in this discussion. Sterling (1949, Figures 7, 8 and 9) illustrated a cuticle type resembling that of the Even Type, although it was verging on being intermediate between the Uneven Type and Even Type. Figure 2-C in Miki & Hikita (1951) also illustrates a cuticle type that is more or less similar to the Even Type. However, the material used by Sterling (1949) and Miki & Hikita (1951) were from *M. glyptostroboides* seedlings (or young trees). As previously mentioned, cuticle morphology varies not only among taxa and between organs, but also between growth stages. Preliminary investigations of the developmental stages of the stomata (Liu *et al.*, 1999) indicated that the stomata might change shape from being circular to oval and finally to rectangular during various developmental stages. This progression is to some extent similar to the change from elliptic (Even Type) to rectangular (Uneven Type) (Table 6-1; Figures 6-1 and 6-2). It is possible that the *M. glyptostroboides* trees possessing Uneven Type cuticle can display Even Type cuticle when they were seedlings (see discussion below), and thus, the aforementioned recommendation that only mature leaf material be used for cuticle analyses of *M. glyptostroboides*, or any other plant for that matter, is a suggestion that should indeed be taken seriously.

In summary, among *M. glyptostroboides* native population the Even Type cuticle is known only from the Paomu Tree, and all other reports of *M. glyptostroboides* cuticle, unless they were obtained from seedlings, possess the Uneven Type cuticle morphology. This is expected because the Paomu Tree was not known until the 1970s (Ling, 1976), and all materials used in the hundreds of reports that were published in the scientific and popular literature were based on the *M. glyptostroboides* trees growing in the Shui-sha-ba Valley, the main distribution area of living *Metasequoia*, or based on cultivated trees with Shui-sha-ba Valley origin. As a result, all of the investigations of mature *M. glyptostroboides* cuticle prior to Leng *et al.,* (2001) display Uneven Type cuticle.

4. CUTICLE OF FOSSIL *METASEQUOIA*

Compared with the quantity and quality of the cuticle studies on *M. glyptostroboides*, those including *Metasequoia* fossils are not only scarce, but also fragmentary. The limited progress of cuticle studies on fossil *Metasequoia* is perhaps due mainly to the difficulty of obtaining fossil *Metasequoia* cuticle and the fact that fossil *Metasequoia* leaves are readily identifiable and the need to use cuticle micromorphology as a taxonomic tool was not as necessary as for many other plant taxa. As a result, cuticle is largely unstudied in fossil *Metasequoia* and only fragmentary data can be found scattered among the vast number of papers of this genus. Moreover, all fossil cuticle characters that were briefly described are based on LM observations (Miki, 1941; Miki & Hikita, 1951; Chaney, 1951; Sveshnikova, 1963, 1975a, 1975b; Takhtajan, 1967; Basinger, 1981; Huggins, 1985; Horiuchi, 1996; Liu *et al*., 1999).

It should be pointed out that the cuticle of "*Metasequoia occidentalis* (Newberry) Chaney", collected from the Wuyun Formation in Jiayin County, Heilongjiang Province, China as shown in Figures 63, 65, 67 and 68 in Liu *et al.* (1999) does not resemble conifer cuticle. The reticulate venation pattern that is clearly visible in Figures 63, 67 and 68 implies a possible angiosperm origin for this cuticle. This is likely the case because the Wuyun Formation yields large quantities of well-preserved compression fossils, which commonly overlap with one another in the sedimentary bedding planes and *Metasequoia* remains are commonly found in association with angiosperm leaves.

Apart from the general taxonomic utility of cuticle characters in the plant fossil record, fossil *Metasequoia* cuticle has also been used to reconstruct the paleo-CO_2 levels of the ancient atmosphere by calculating the leaf stomatal index (SI) (Royer, 2001, 2002, 2003; Royer *et al.*, 2001a, 2001b, 2002). However, given the difficulties in obtaining fossil *Metasequoia* cuticle this usage is still in its infancy. It is worthy of mentioning, however, that the species-specific inverse relation between atmospheric CO_2 concentration and stomatal density (SD) or stomatal index (SI) for many woody angiosperm species has been long confirmed, but such a relation for conifers has not been fully demonstrated. New experiments indicate that the atmospheric CO_2 concentration might be related to stomatal frequency in conifers based on the number of stomata per millimeter of needle length, rather than SD or SI (Kouwenberg *et al.*, 2003). Thus the use of fossil *Metasequoia* leaf SI as a proxy for paleo-CO_2 reconstruction may need further confirmation. Moreover, the relationship between the atmospheric CO_2 concentration and stomatal frequency is species-specific, and in addition, it is possible that a single species may develop different stomatal behavior through time (Royer, 2001). Therefore, caution should be exercised in selecting taxa for such analyses. *Metasequoia* was believed to be an evolutionary conservative taxon mainly based on the lack of significant differences in the gross morphological features observed in fossil and living *Metasequoia*. Based on this notion *Metasequoia* was considered to be a suitable candidate for determining paleo-CO_2 levels. However the discovery of different cuticle types (Leng *et al.*, 2001) places some question as to the reliability of these reports.

5. EVOLUTIONARY IMPLICATIONS

Cuticle morphology has long been used to interpret the evolutionary history of certain taxa (e.g., Florin, 1951). Previous comparisons of fossil and living *Metasequoia* cuticle characters were preliminarily carried out at the LM level (Sveshnikova, 1963, 1975a, 1975b; Basinger, 1981; Huggins, 1985). However, given that different types of cuticle in *M. glyptostroboides* were only recently recognized (Leng *et al.*, 2001), the evolutionary implications of these differences have not yet been sufficiently addressed. Previous studies were restricted to searching for cuticle characters that could be used to separate living and fossil *Metasequoia* cuticle and differences between living and fossil cuticle, including differing degrees of anticlinal wall undulation, variation in the number of stomatal rows within a stomatal zone and different size ranges of the cells were reported. However, a comprehensive survey of the literature and a synthetic analysis of the results have revealed that those differences were likely due to insufficient observations on a limited sample size because from a broader perspective, they all fall within the same range of variation seen in both the living and fossil representatives and bear little taxonomic value for species discrimination. The low resolution of LM compared to SEM further compounded the problem. In addition, those variations are reported to be related to environmental factors or developmental stages. For example, leaf maturity and moisture can largely control the degree of anticlinal wall undulation. The number of stomatal rows within a stomatal zone may vary from one position to another on the same leaf blade as well as be affected by climatic conditions, whereas the size of the epidermal cells can be related to leaf maturity and nutrition (Stace, 1965, 1984; Leng *et al*., 2001). As such, all are considered to be of little taxonomic value. However, SEM observations have allowed the recognition of two types of cuticle within *M. glyptostroboides*, the Uneven Type and Even Type, which promote the evolutionary implications of cuticle morphology to a more promising state.

To approach this goal, the evolutionary history of these two cuticle types is traced in the fossil record through an extensive literature survey as well as additional detailed SEM studies of fossil *Metasequoia* cuticle. Preliminary results indicate that some figures or illustrations in previously published papers, although all based on LM observations, show evidence of their cuticle type, and strikingly, all of the cuticle examined that allow recognition of cuticle type, belong to the Even Type group (e.g., Figure 8-F in Miki, 1941; Figures 2-A and 2-B in Miki & Hikita, 1951; Plate II, Figure 8 in Sveshnikova, 1963; Plate VI, Figures 8, 9, 10, and 11 and Plate VII, Figures 2, 3, and 4 in Takhtajan, 1967; Plate I, Figures 5 and 6 in Sveshnikova, 1975a; Plate III, Figure 6 in Sveshnikova, 1975b; Figure 70 in Basinger, 1981; Plate 7, Figures 1 and 2 in Huggins, 1985; and Figure 20-4 in Horiuchi, 1996).

Given that this conclusion was based only on LM images, and in some cases from blurred images, the reliability of these results requires direct examination of the specimens themselves. Available SEM data of well-preserved *Metasequoia* from the Miocene Clarkia deposit, Idaho, USA, and the late Paleocene-early Eocene Iceberg Bay Formation from Stenkul Fiord, Ellesmere Island, Nunavut, Canada (Figures 6-4, 6-5 and 6-6) display the Even Type cuticle, a result that is consistent with those of the literature survey.

Based on the available data, which show that the Even Type cuticle is common in the fossil record of *Metasequoia*, but is now represented only by the Paomu Tree, and possibly in seedlings of other trees, a hypothesis has emerged. That is, the Paomu Tree is a relict of the once widespread ancestral population and should be viewed as the true “living fossil” of the genus, while the other representatives of the living population in South-central China are the result of geologically recent mutation(s). It is worthy of mentioning that this hypothesis has been supported by a preliminary DNA analysis of living

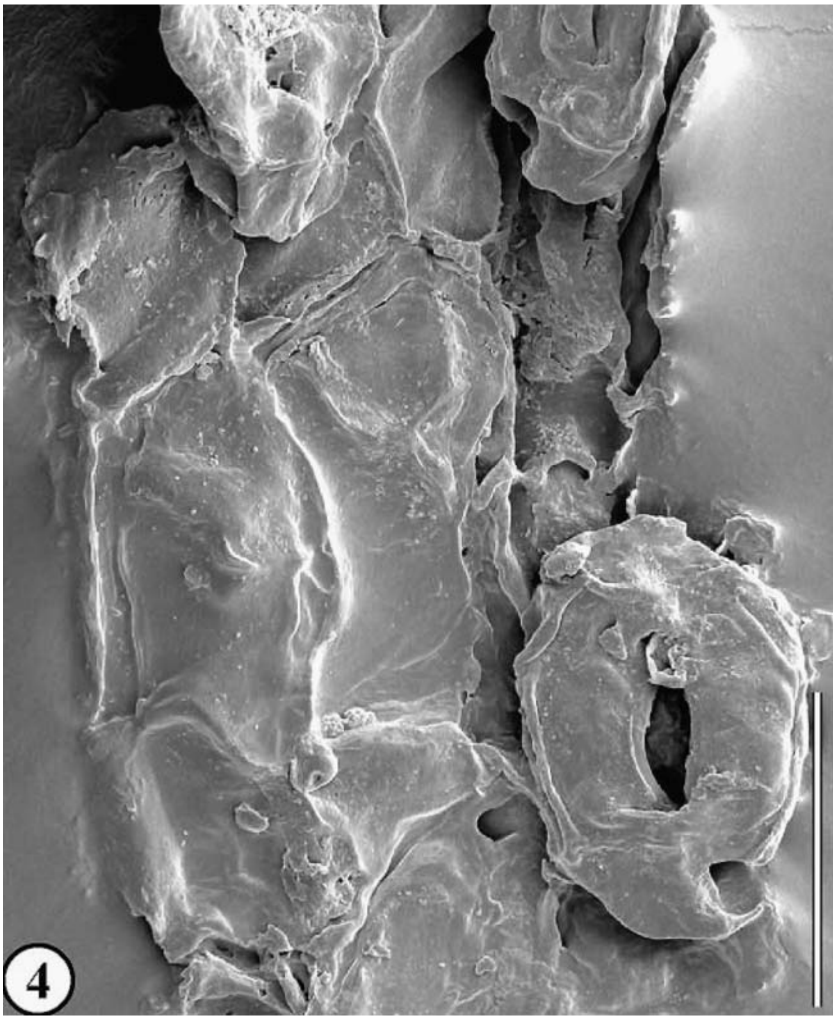

Figure 6-4. Even Type of cuticle characterized in a fossil *Metasequoia* leaf from the late Paleocene-early Eocene, Ellesmere Island, Nunavut, Canada (internal surface of the stomatal zone), showing two elliptic stomata and rectangular epidermal cells. Scale bar = 30 μm.

M. glyptostroboides leaves from their native populations in which the Paomu Tree was shown to be basal to all other *M. glyptostroboides* trees so far sampled (Li & Yang, 2003).

The fact that the geologically older Even Type cuticle observed in fossil *Metasequoia* leaves can be evident in the juvenile stage(s) of *M. glyptostroboides* living trees, but becomes replaced by Uneven Type cuticle when the trees mature is of considerable interest given that it may represent another

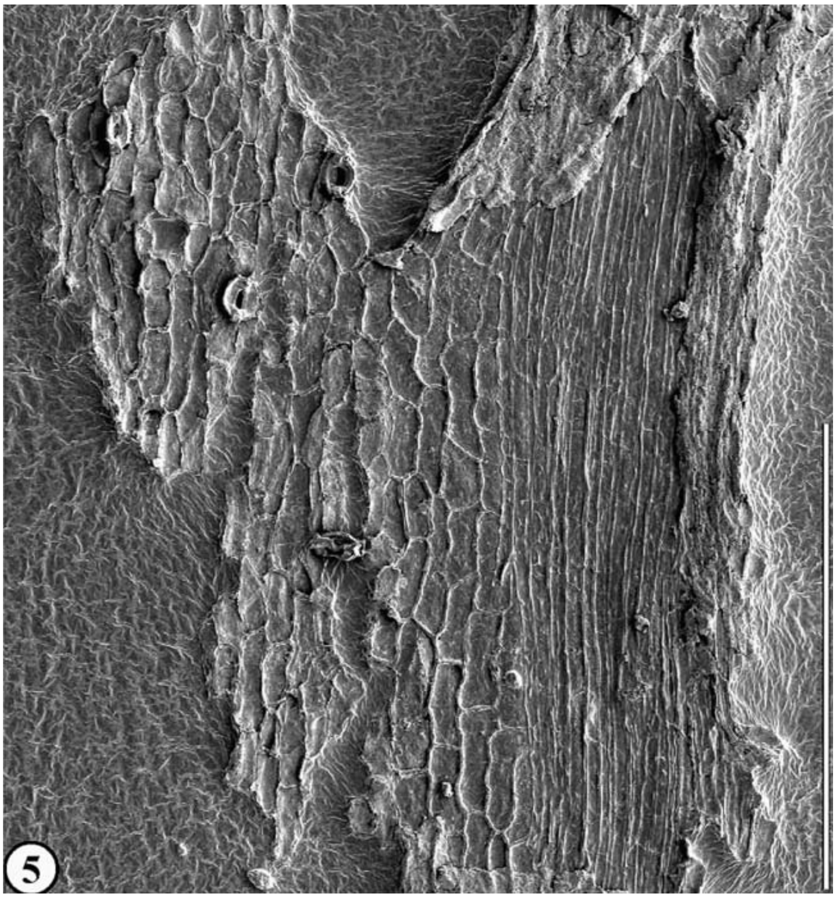

Figure 6-5. Even Type of cuticle characterized in a fossil *Metasequoia* leaf from the Miocene Clarkia deposit, Idaho, USA, showing stomatal (left), non-stomatal zones (middle) and the area of the midrib (right). In the stomatal zone the stomata are elliptic and the epidermal cells are rectangular. Scale bar = 300 μm.

example of ontogeny recapitulating phylogeny (Freeman & Herron, 2001; Gould, 1977) and warrants further study.

It should be noted that although the above-mentioned hypothesis is formed based on the micromorphological evolution traced in fossil record, the ontogenetic data provided by juvenile *M. glyptostroboides* tree leaves, and a preliminary molecular phylogenetic analysis, additional study is needed to support or refute this hypothesis. This includes a more complete study of the *Metasequoia* fossil record to trace the geologic history of the two known cuticle types, a better resolved molecular phylogenetic analysis based on samples representing all native groves of the population, and studies on the environmental impact on cuticle morphology, which could preclude the possibility of phynotypic

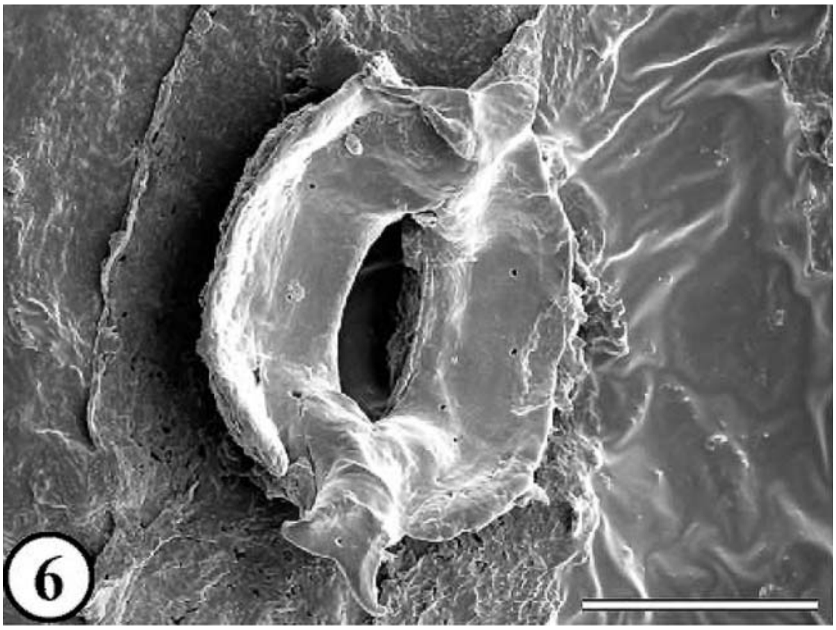

Figure 6-6. A stoma enlarged from the fossil *Metasequoia* leaf of the Miocene Clarkia deposit from Idaho, USA that is illustrated in Figure 6-5. Scale bar = 15 μm.

adaptation of cuticle characters (i.e., environmentally controlled cuticle variation). If this hypothesis is further substantiated, a number of questions will certainly then emerge. For example, did other new characters evolve? Did these new characters facilitate the adaptation of mutated *Metasequoia* to Quaternary climate enabling its survival? Is the main living *Metasequoia* population in the process of evolving into a new species? The answers to these questions will undoubtedly shed further light on the evolutionary interpretation and conservation of this endangered genus.

6. CONCLUSIONS AND PROSPECTS

Since SEM methodology was first introduced to cuticle analyses in 1960s–1970s (Heywood, 1971), it has become a powerful tool and played an important role in recognizing the two distinct cuticle types in the living *M. glyptostroboides* population, the Uneven Type and Even Type. The analysis of the distribution of the two cuticle types in living and fossil *Metasequoia* leaves has revealed significant evolutionary implications that may shed light on the phytogeographic history of the genus. Moreover, further research into poorly known and remote natural groves of *M. glyptostroboides* may reveal new and genetically distinct trees such as the recently discovered tree in Paomu Village.

However, it should be noted that although the recognition of two cuticle types was based on a comprehensive study of the living *M. glyptostroboides* population (Leng *et al.*, 2001) and the antiquity of the Even Type cuticle has been supported by a recent molecular analysis (Li & Yang, 2002), the currently available data on fossil cuticle are still limited and the evolutionary implications of these two cuticle types should be considered tentative. Future studies that might help confirm or refute these notions include:

(1) Detailed studies, particularly SEM studies, of the cuticle characters in the whole fossil record through geologic time to completely trace the origin and evolution history of different cuticle types.

(2) Observations of the changes in cuticle characters through developmental stages of individual trees that will further elucidate the putative ontogenetic relationships. The ontogeny recapitulating phylogeny proposal was based only on previous reports of Sterling (1949) and Miki & Hikita (1951) of LM observations and thus requires further confirmation.

(3) An enlarged sample size and study of the native *M. glyptostroboides* population Leng *et al.* (2001) attempted to obtain samples of trees from every natural grove of *M. glyptostroboides* population in South-central China that were accessible at the time. However, according to Ling (1976) several large trees were found in 1970s from other remote areas in Hunan Province and Sichuan Province (now a part of Chongqing Municipality Directly Under the Central Government), although none of those trees have been officially documented. A search for more individual natural trees possessing the rare Even Type cuticle is not only essential for interpreting the evolutionary history of the genus, but might help to increase the known morphological and genetic diversity of this endangered species. Thus, a new round of searching for more native *M. glyptostroboides* trees in China, particularly in the mountain regions that are peripheral to the Shui-sha-ba Valley is urgently needed.

(4) Observations on other possible character differences (cuticle or non-cuticle) between the Paomu tree and other trees, and their relationship with different environmental factors. We have realized that the mutation(s), which may be responsible for the Uneven Type cuticle might have played an important role in the survival of *Metasequoia* in South-central China. However, what characters might have helped *Metasequoia* trees to be more adaptive to the cold weather during the Quaternary and how they functioned are still open questions.

Although the genus *Metasequoia* is easily recognized among other fossil (e.g., *Sequoia*, *Taxodium*, *Parataxodium* Arnold *et* Lowther), the classification and identification of *Metasequoia* fossils at the species level, has been shown to be difficult unless a large number of specimens from various organs are available for comprehensive investigation (Basinger, 1981, 1984; Stockey *et al*., 2001). As a result, the classification of fossil *Metasequoia* is an issue of high controversy. More than twenty fossil species of *Metasequoia* have been established throughout history, and most have been merged into one species, *M. occidentalis* (Christophel, 1976; Liu *et al*., 1999; LePage *et al*., this volume), leaving only two other valid fossil species, *M.milleri* Rothwell *et* Basinger (1979) and *M.foxii* Stockey *et al*. (2001). Cuticle analysis has played a very limited role in the taxonomic revision of *Metasequoia* fossils, mainly due to the difficulty of obtaining cuticle from *Metasequoia* fossil leaves. In addition, the comprehensive SEM observations of *M. glyptostroboides* leaves (Leng *et al*., 2001) indicate that a considerable amount of detail is lost when LM is the only tool used for micromorphological observations. It is believed that cuticle analysis based on SEM observations will be highly promising for the future study of the taxonomy of *Metasequoia* fossils, at the species or intra-specific levels.

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Chapter 7

Ultrastructural Preservation in Middle Eocene *Metasequoia* Leaf Tissues from the Buchanan Lake Formation

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Abstract: Mummified leaflets of middle Eocene *Metasequoia* Miki sampled at 5 mm vertical intervals from a section of lignite extracted from the Upper Coal member of the Buchanan Lake Formation at Napartulik on Axel Heiberg Island were examined via transmission electron microscopy (TEM) to quantitatively and qualitatively assess the extent of sub-cellular preservation. The presence of chloroplasts and chloroplast constituents were tallied on a per cross-section

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basis, with equal examination time allotted to each cross-section. Features of note were stacked membranes, appressed membranes (grana), associated membranes, disassociated membranes, vesicular membranes, lipid droplets, starch grains and amorphous breakdown lipids. The size and shape of each organelle was measured, as well as the orientation. Intact chloroplasts were observed in 41.6% of the fossil leaves examined, and in 66.6% of the 5 mm intervals. In 27.7% of the leaves, the chloroplasts were so well preserved that features related to thylakoid geometry (degree of grana stacking, number of thylakoids per granum, stack width) were measurable. By performing a nested multivariate analysis of variance, significant differences in preservation were observed between individual leaflets as well as between vertical intervals. An apparent oscillation in preservation quality with an estimated period of 62.5 years was distinguished using the chloroplast features found to best discriminate between layers of lignite.The predominantly observed elliptical shape of the chloroplasts was deemed in general not to be the result of compression, but rather representative of the original geometry upon abscission, based upon the standard deviation of the orientation of the chloroplasts within each leaflet cross section. Where discernible, thylakoid features were used to classify the fossil leaflets as originating from high or low-light environments. Between 67 and 78% of the leaflets were classified as 'shade-types.'

Key words: Axel Heiberg Island; Buchanan Lake Formation; chloroplast; Eocene; fossil; lignite; mummification; Napartulik; sun and shade type leaves; thylakoid; ultrastructure.

1. INTRODUCTION

The 'Level N' lignite of the Upper Coal Member of the middle Eocene Buchanan Lake Formation at Napartulik, Axel Heiberg Island, Canadian High Arctic, is composed of exceedingly well-preserved leaves and twigs of the conifers *Metasequoia* Miki and *Glyptostrobus* Endlicher (Basinger, 1991). The autochthonous leaf litter mats found in these forested horizons represent the ancient forest floors of floodplains and the associated poorly-drained swamps (Ricketts, 1986, 1991; Basinger, 1991). As these vegetative materials were reported to have been subjected to relatively no chemical or biological alteration (Obst *et al.*, 1991) since their deposition approximately 45 million years ago (Ma), it followed that a study focused on the extent of preservation at the ultrastructural scale could provide new information on the paleo-environmental conditions at the site, especially in relation to the yet undetermined mechanism(s) of preservation.

The precedent for studies of fossil leaf ultrastructure was set primarily by Karl Niklas from the late seventies to the early nineties, on the Miocene angiosperm floral remains from the Clarkia and Succor Creek floras of Idaho and Oregon. This research provided a basis for quantifying organelle survival under diverse geologic conditions of preservation via an index of fidelity to the presumed living state (Niklas *et al.*, 1985). Specific cellular features including the endoplasmic reticulum and Golgi bodies, nuclei, mitochondria, chloroplasts, starch grains, cell wall and the cuticle were each assigned a numerical value and the fidelity index of a tissue represented the sum of the values for each component present in more than 50% of the total cells observed. Perhaps the most surprising findings from this work were that the fossil chloroplasts appeared to be preferentially preserved over the nuclei and that both were rarely preserved in the same cell.

More recently, research on the late Eocene Pasekovo flora of the Central Russian Upland has revealed astounding preservation of chloroplast ultrastructure to the extent that even the arrangement of the thylakoids, the internal membranes of the chloroplast, into grana stacks is distinct in extracts taken from the compressed leaves of *Rhodomyrtophyllum pasekovicum* Vickulin (Vikulin, 1999). Also remarkable is the preservation of virtually all organelles and their internal structure in leaf compressions of the Eucommiaceae from the Miocene of Kazakhstan (Zhilin & Yakoleva, 1994).

The presence of intact organelles in ancient leaf tissues is surprising considering the chemical and taphonomic processes that take place in leaves either during senescence or after detachment that has been induced by some trauma. The breakdown patterns are quite different in each case and implies an extremely rapid, natural preservation process that not only arrested all catabolic activities, but also prevented microbial attack. Additionally, the leaf tissues could not have completely undergone senescence before abscission, as is evident from the pattern of breakdown observed during that process, in which the organelles would not have persisted. Specifically, the observations on chloroplast and nucleus preservation in the Miocene Clarkia leaf compressions had to be reconciled with the observed ultrastructural stability of the various protoplasmic components during senescence or necrosis, where the plastids typically disappear before nuclear disorganization takes place (Woolhouse & Batt, 1976). The bias was thus initially difficult to explain since, even if post-depositional conditions favored chloroplast preservation over the nuclei, the chloroplasts should typically already have been destroyed before the nuclei as a result of senescence or necrosis. Niklas (1983) ultimately attributed this phenomenon to protoplast partitioning, whereby the nucleus, which controls the senescence process in the cell, is isolated from the chloroplasts as a result of osmotic shock. Issues relating to senescence, abscission and the preservation of fossil organelles are discussed in detail later in the chapter in relation to the ultrastructural preservation observed in the *Metasequoia* litter samples from Axel Heiberg Island.

The investigation of the ultrastructural preservation in the middle Eocene *Metasequoia* leaflets consisted of three parts. The first component involved a qualitative examination via transmission electron microscopy (TEM) of a statistically viable sampling of leaflet cross sections taken over a vertical gradient in a lignite block to assess the overall quality of preservation, determine the general features of interest and establish the properties to which a quantitative assessment could be applied. Consequently, the second component consisted of a quantitative assessment of chloroplast preservation in the fossil leaflets, and the third part centered on the classification of those samples as sun or shade-type leaves based on several thylakoid features of the preserved chloroplasts. This last component required a separate study of the properties of sun and shade leaves in modern *Metasequoia glyptostroboides* Hu *et* Cheng to quantitatively establish the response of *M. glyptostroboides* leaflets to high- and low-light environments in terms of features found to be preserved in the fossils. Aspects of this work, though in less detail have been discussed previously in Schoenhut *et al.* (2004).

2. METHODS AND MATERIALS

A 60 mm thick block of frozen mummified fossil *Metasequoia* litter (approximately 250 mm^2 in area) was divided into twelve vertical 5 mm layers. Each layer was floated in a shallow pan of deionized water and gently agitated to free individual leaflets and branches. Leaflets were chosen from separate branches and rinsed to remove clay and other debris. The leaflets were then rehydrated in 100, 80 and 50% alcohol for 15 min each. After washing in phosphate-buffered saline (PBS), the leaflets were transferred to a solution of 4% paraform and 1% glutaraldehyde and left overnight at 4°C. The next morning the specimens were transferred to 5% glutaraldehyde for 2 hr at room temp. The solution was then changed and 1% tannic acid was added to the fixative and left for 4 hr. Specimens were then washed three times with 0.1M sodium cacodylate buffer (NaCaC), at room temperature. The glutaraldehyde was removed from the samples before adding the osmium. The samples were transferred to a glass vial and osmicated with 2% osmium in 0.1M NaCaC for two 60 min changes. Samples were then washed two times with 0.1 M NaCaC and twice with deionized water. The samples were then stained enbloc with 2% aqueous uranyl acetate for 30 min before washing three times in deionized water. Dehydration was accomplished in 50%, 70%, 80%, 90% and 100% ten min changes of ethanol. The specimens were then placed in 1:1 ethanol:propylene oxide for 5 min, followed by two five min changes to absolute propylene oxide. Infiltration was accomplished by successively placing samples in 3:1, 1:1 and 1:3 propylene oxide (PO):EPON 812 for forty-five min each. After a change to 100% EPON for sixty min, samples were placed in fresh EPON and left overnight at 4°C. The next day, after warming to room temperature, the solution was replaced with fresh EPON, using a rotator to infiltrate. The samples were cured at 70°C for 48 hr. Sections were cut to a thickness of 700 Å using a Leica Ultracut S microtome and mounted on 200 mesh bar copper grids. The grids were stained for 15 min at room temperature in 7% uranyl acetate in 50% ethanol, washed in deionized water and counterstained in Bismuth subnitrite for 15 min at room temperature before being washed in deionized water and left to dry.

The samples were examined using a 100cx JEOL transmission electron microscope at magnifications of up to 150,000x. Preparation of the samples for TEM and fixation through mounting and staining was performed by the staff of the Bio-Imaging Core facility at the University of Pennsylvania. A Phillips EM420 TEM enabled a spectroscopic analysis of element distribution (Kevex Delta 1) to be performed so that the composition of the apparent biofilm coating the leaf surfaces could be determined.

The original intent of this research was to employ the method for quantifying organelle ultrastructural integrity that had been applied to the Clarkia leaf compressions to provide a means for contrasting the preservation at that site with that at Axel Heiberg Island. However, it was not possible to do so because the cell wall integrity had not been maintained for the mesophyll cells in the Axel Heiberg samples. Only the epidermal and vascular cells had survived the combined effects of compression and decomposition. Instead it became necessary to examine the mesophyll area, which consisted of fragments of the failed cell walls and organelles suspended in what appeared to be a tannin-rich matrix. Additionally, with few exceptions it was found that the only organelles preserved were the chloroplasts (or chloroplast remnants) in various conditions. The method of investigation thus had to be amended to quantify the various states of chloroplast preservation observed by identifying a number of distinct features, the presence of which could be tallied on a per section basis.

Three sections from each leaflet were examined and three leaflets from each of the twelve 5 mm intervals were considered for a total of 108 sections and 36 leaflets. Each section was examined for 45 min. Chloroplasts and chloroplast constituents were photographed and counted. The length and width of all intact chloroplasts were measured, as well as the orientation of the long axis of the organelles. Measurements of orientation were always carried out at the same magnification. The condition of each chloroplast (or constituent) was recorded in terms of the presence of stacked membranes, grana, associated and disassociated membranes, lipid droplets, amorphous breakdown lipids and evidence of starch grains (areas clearly once occupied by starch grains that deteriorated in place).

The number of times each feature was observed for each section was recorded. The maximum section thickness was also measured. These data were used to perform individual nested ANOVAs for each feature and a nested multivariate analysis of variance (MANOVA) to assess whether there was a significant difference in preservation between litter layers and between individual leaflets. The between leaflet effect was considered to be nested within the layer effect. The within leaflet (between cross section) variance was used as the residual (error) mean square.

Chloroplast shape, which was defined as the length to width ratio, was determined and the means and standard deviations were calculated for each section and leaflet. The standard deviation of the orientations of each chloroplast within the section was also calculated. This was intended to detect whether the observed shape of the fossil chloroplasts was reflective of the original geometry or due to the effects of compression-related deformation. A low standard deviation of the angles of orientation for the chloroplasts within a leaflet section would indicate that the shape was likely due to compression, as directional stress would reorient all of the chloroplasts such that the long axes would be perpendicular to the direction of stress. A high standard deviation of the angles of orientation would indicate that the orientation was essentially random and the observed geometry was not produced by stress. Similar measurements were made on randomly chosen chloroplasts in sections of an equivalent number of fresh green leaflets of *M. glyptostroboides* for comparison.

In samples where the preservation of the chloroplast ultrastructure was found to be sufficient, the following measurements were made for each intact chloroplast: (1) minimum number of thylakoids in a stack; (2) maximum number of thylakoids in a stack; (3) minimum number of grana in a stack; (4) maximum number of grana in a stack; (5) minimum number of thylakoids per granum; (6) maximum number of thylakoids per granum; and (7) average width of the grana stacks.

These measurements were then used to perform a classification analysis employing the minimum chi-square rule. The established means for the sun and shade type leaves were established from measurements made on leaflets of the nearest living relative, *M. glyptostroboides*. Fresh leaflets were collected from the *M. glyptostroboides* grove at the Morris Arboretum, Philadelphia Pennsylvania in early May and October. Samples were taken from six different trees. “Shade” leaves were taken from the lowest branches, closest to the trunk. “Sun” leaves were taken from positions farthest from the trunk, at a height of approximately 3 m above the ground surface. Notes were made for each tree as to its general position and environment, for example, whether it was shaded by taller trees or growing at the perimeter of the grove so that the tree was fully exposed to sunlight on that side. Three leaflets from each light environment were selected for each of the six trees. The leaflets were refrigerated immediately after collection and placed in 5% glutaraldehyde (pH 7.4, 0.1 M cacodylate buffer) within 24 hr. These samples were prepared for TEM using the same procedure applied to the fossil leaflets except that re-hydration, tannic acid fixation and infiltration using propylene oxide was not necessary.

Ten random chloroplasts were selected from each leaflet and measurements consistent with those taken on the fossil samples were made. The stack width was taken as an average of the numerous grana stacks within each chloroplast. The minimum and maximum number of thylakoids per stack, thylakoids per granum and grana per stack were recorded for each chloroplast. In a chloroplast with numerous unstacked (stromal) thylakoids, the minimum number was recorded as “1” for each of the aforementioned categories, essentially signifying “no stacking”. The data were assessed using individual analyses of variance for each feature, as well as a multivariate analysis. In both the univariate and multivariate analyses, each of the features were found to vary significantly ($P < 0.001$).

The data from the experiment on modern *M. glyptostroboides* leaves that were sampled in October were used to create the within-group dispersion matrix for the classification analysis and to obtain the means for each feature characteristic of the “sun” or “shade” groups. The chi-square for each fossil leaflet with respect to the two groups was then computed. The leaflet was then assigned to the group for which it had exhibited the lowest chi-square value. The analysis was repeated several times, with modifications to the features assessed. A final group assignment was made based in the results from the various analyses.

3. QUALITATIVE OBSERVATIONS ON FOSSIL LEAF ULTRASTRUCTURE

Typical examples of fossil leaflet cross sections are shown in Figure 7-1. Only the cells of the epidermis and vascular bundle are generally found intact. The cell walls of the spongy mesophyll and palisade cells are most frequently

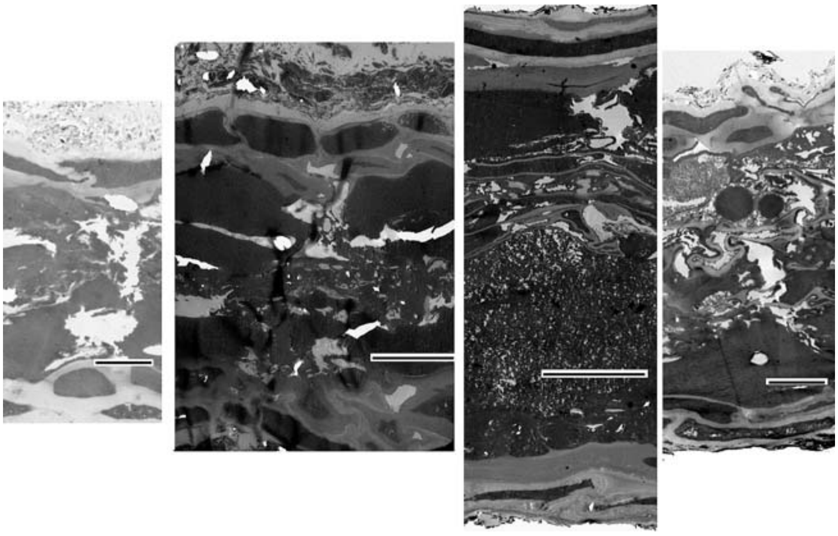

Figure 7-1. Typical cross sections of the fossil *Metasequoia* leaflets. Scale bars = 10μm.

found to have ruptured, presumably as the result of senescence-related lyses, post-depositional osmotic shock or failure under tension resulting from the transfer of compressive stresses from overburden weight. The epidermal cells are distinct due to the highly lignified cell walls and the tanniferous inclusions filling the otherwise hollow cells. When observed via TEM, the tannins are electron dense and appear dark gray. The epidermal cells have clearly been reshaped to varying extents by compressive stress. Commonly bereft of contents, the vascular cells also tend to be deformed in a manner characteristic of the effects of compression; though the cell walls are intact, the cells have collapsed and are flattened. It is of note that where cells are clearly occupied by tannins, the shape change has been less extensive. The mesophyll area consists of the remnants of ruptured cell walls apparently suspended in a tanniferous matrix. The abundance of tannins within the mummified leaflets is consistent with the observations made on other fossil leaf tissues by Niklas & Brown (1981), Vikulin (1999) and Zhilin & Yakoleva (1994), as well as those on modern peats by Cohen & Spackman (1977). However, these tanniferous inclusions are far more abundant in the fossil leaflets than in leaflets from living *M. glyptostroboides* litter collected from managed groves in Pennsylvania and New Jersey and decaying under circumstances varying in acidity, dissolved oxygen availability and temperature. Even in modern litter that has been deposited into an aqueous environment artificially enriched with tannic acid, the epidermal cells were only partially filled with tannin inclusions, while the mesophyll cells were sparsely occupied by round tannin bodies of variable size. This disparity can perhaps be attributed to the influence of environmental conditions during the development and senescence of the leaf. Observations confirm that in the leaves of trees subject to environmental stresses such as higher levels of solar radiation, reduced nutrient availability or high wind-induced evapo-transpiration rates, the tannins completely filled the vacuoles of the epidermal and palisade mesophyll cells by the end of the growing season, whereas tannins were only moderately present in the leaves of trees grown under optimal conditions (Bussotti *et al.*, 1998). The period of constant daylight during the growing season to which the middle Eocene *Metasequoia* were subject may have produced the observed excess of tannins in the fossil leaflets.

The excellent quality of ultrastructural preservation in the mummified leaf tissues indicates that microbially mediated degradation was not effectively operational, although bacteria are clearly present in abundance on the leaf surfaces and within the epidermis. Bacilli were found in a majority of the leaves, while flagellated bacilli and spirilla were observed far less frequently. Bacilli were typically found in abundance only on the leaf surface, although some epidermal cells appeared to have been invaded by individual rods. Bacilli and associated biofilm components were also observed within the mesophyll only where the overall leaf structure had been ruptured. Mineralized films composed primarily of illite and/or smectite were bound to the cuticle on all of the leaves.

Identifiable organelles and organelle components were most frequently located within the mesophyll area and were often in proximity to large regions of amorphous breakdown lipids. At the perimeter of these lipid rich regions, which demonstrate a negative contrast under TEM (they are electron lucent), stacked and vesicular thylakoid membranes were frequently evident, suggesting that the amorphous areas were originally clusters of chloroplasts. Intact chloroplasts and chloroplast remnants were the most frequently encountered recognizable organelle and were identified in a majority of the leaflets examined.

4. CONDITION OF PRESERVED CHLOROPLASTS AND COMPONENTS

Chloroplasts were observed to be in various states of degradation. The least degraded chloroplasts, those closest in appearance to those seen in fresh tissues, possessed intact double membrane envelopes and grana stacks, with both stromal and granal thylakoids clearly being discernable (Figure 7-2). Lipid

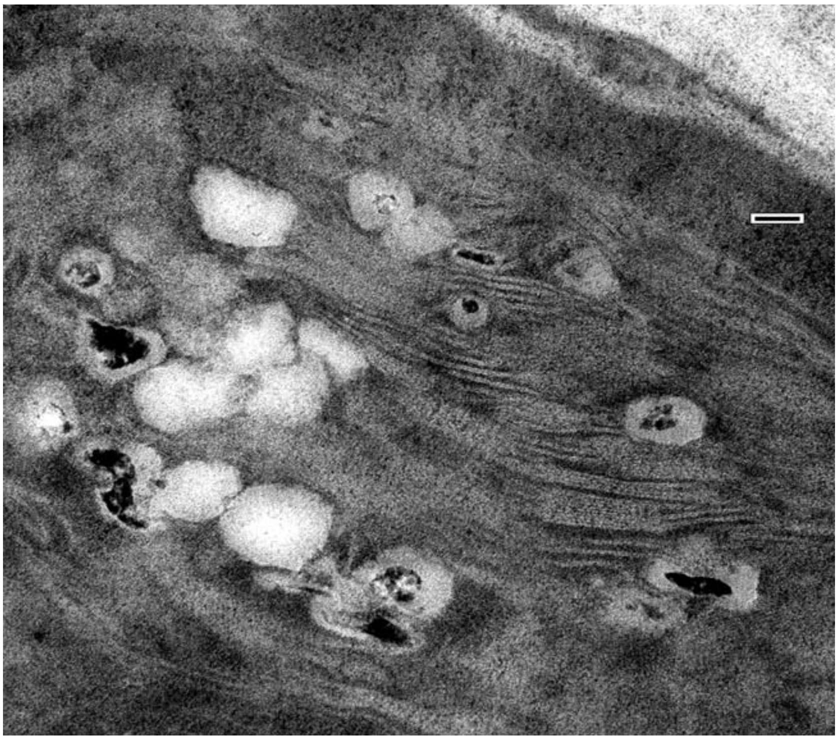

Figure 7-2. Intact chloroplast with grana stacks and lipid droplets are evident. The centers of the lipid droplets stain positively. Scale bar = 100nm.

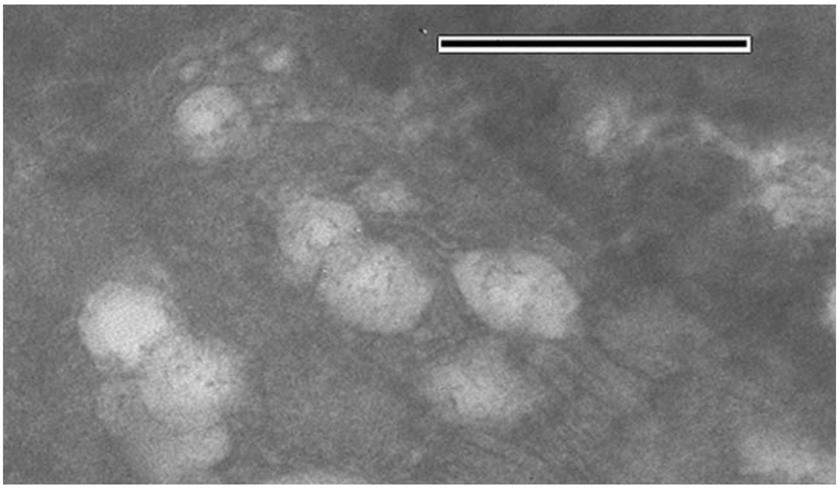

Figure 7-3. Grana stacks that have fused into globuli. Linear traces of the thylakoids are still apparent. Scale bar = 500nm.

droplets and evidence of starch bodies were also frequently present. All membranes stained negatively; however, lipid droplets stained positively near the center and areas that were once occupied by starch grains demonstrated limited positive staining at the periphery. These chloroplasts of high fidelity to the living state were found isolated, in large irregular clusters and in bands.

Chloroplasts in a slightly more advanced state of degradation possessed grana stacks that had fused into lipid rich globuli. It was evident that this had occurred because in less mature globuli, linear traces from the individual thylakoid membranes of the original grana stack were still visible (Figure 7-3).

Stromal thylakoids liberated by the fusion of grana into globuli were observed to: (1) become more closely stacked, possibly as the result of dehydration or compression; (2) pinch off into vesicles; (3) swell, become unstacked and disperse into the stroma or if the chloroplast envelope had been ruptured, into the tanniferous matrix; or (4) remain relatively unchanged such that the stromal lamellae continued to be in association with the globuli.

Closely stacked stromal thylakoids were observed to pinch off into vesicles, which eventually fused into globuli, just as the original grana stacks had. The disassociated membranes were also observed to have broken off into single layer vesicles. Single and stacked membrane vesicles are depicted in Figure 7-4. Membranes that disassociated and dispersed into the tanniferous matrix are shown in Figure 7-5.

Large clusters or linear groupings of chloroplasts appeared to have been subject to membrane fusion from the center out, such that distinct granal and stromal thylakoids and even intact chloroplasts, are evident along the periphery of otherwise occluded, negatively staining areas (Figure 7-6). Individual

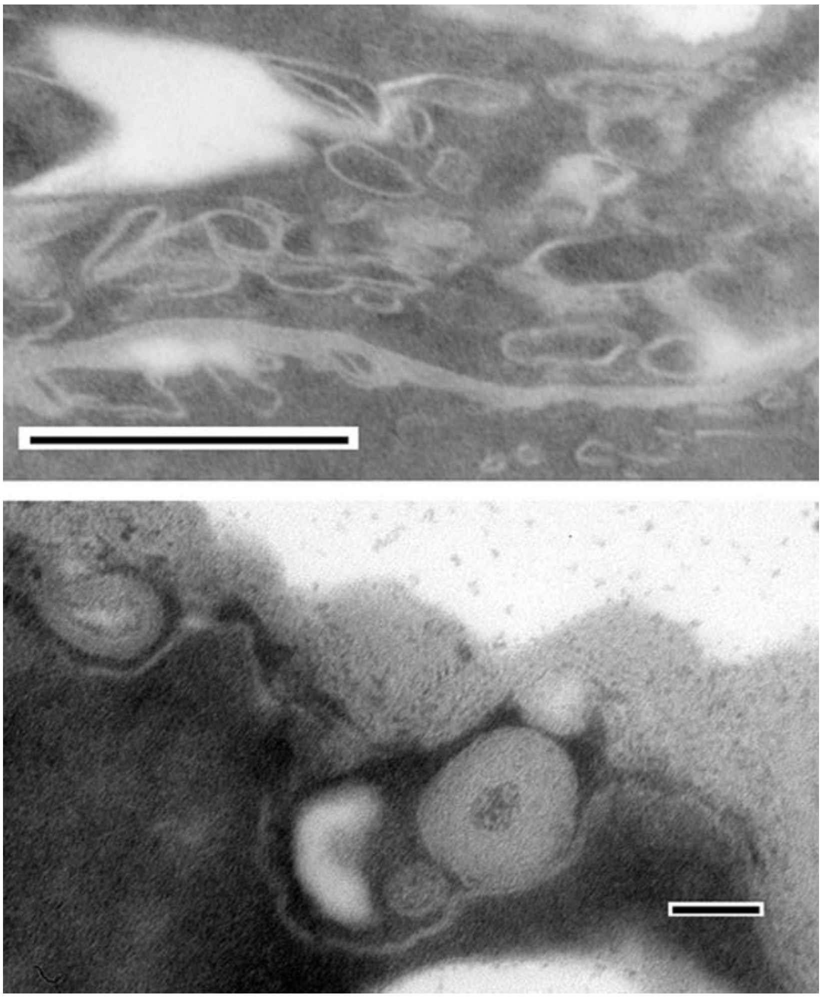

Figure 7-4. Vesicles of single and stacked thylakoid membranes. Scale bar (top) = 500nm. Scale bar (bottom) = 100nm.

chloroplasts frequently were observed to encompass regions of amorphous break down lipids.

5. NEGATIVE STAINING OF THE CHLOROPLAST MEMBRANES

Though there have been few studies of cellular ultrastructure in fossil leaf materials, these examinations have consistently observed the phenomenon of negative staining of the organelle membranes, particularly those of the

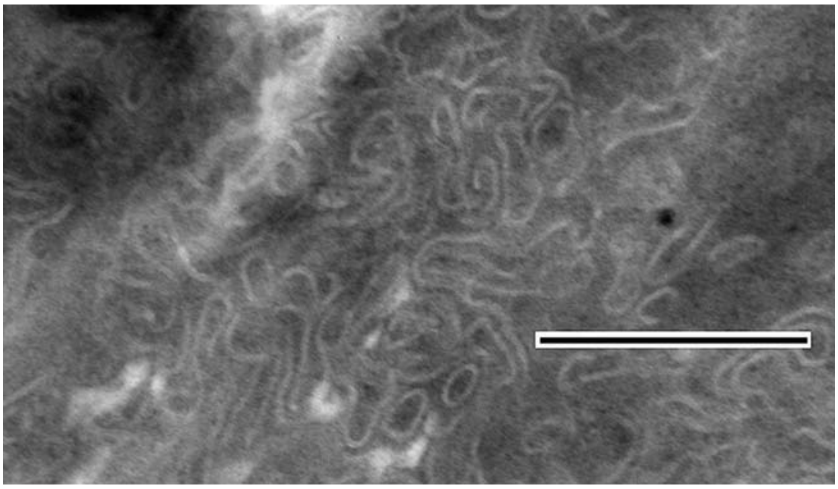

Figure 7-5. Disassociated membranes dispersed into the tanniferous matrix. Some vesicle formation is also evident. Scale bar = 500nm.

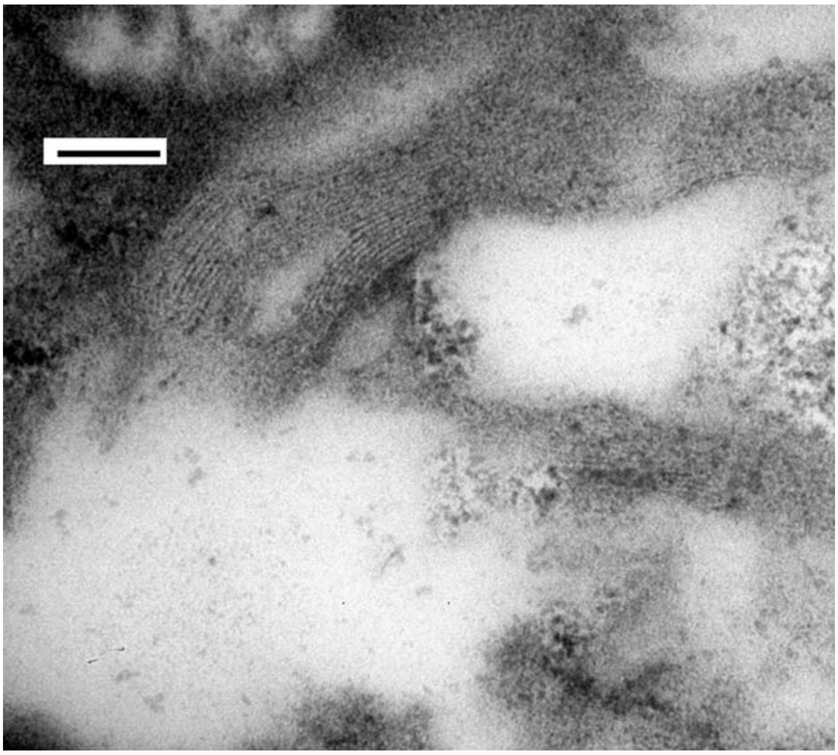

Figure 7-6. Stacked membranes at the periphery of a large area of amorphous breakdown lipids. Scale bar = 100nm.

chloroplast. The precise mechanism behind this alteration of the staining properties of these membranes has yet to be established. Zhilin & Yakovleva (1994), reported the preservation of organelles to an extent comparable to the living state in Miocene leaf compressions of *Eucommia palaeoulmoides* Zhilin *et* Yakovleva, and attributed the negative contrast to the replacement of organic substances with mineral ones. In this manner, the membranes themselves are not present, but represent merely "shadows of, or places once occupied by" the membranes. They also observed normal staining (contrast) of the membranes not associated with organelles, but rather located near lipid-like sediments. This was interpreted to indicate that the lipid components were better preserved than proteins in the fossil material.

Alternately, based on observations from an extensive TEM study of leaf compressions of numerous taxa from the Miocene Clarkia deposits, Niklas *et al.* (1985) suggested dehydration as the mechanism responsible for the reorganization of the membranes exhibiting negative staining. When applied to modern tissues, dehydration followed by tannic acid fixation resulted in a negative contrast (Niklas *et al.*, 1985). As described by Luzzati & Husson (1962), 80% dehydration caused the rearrangement of the phospholipid components of the membranes into hexagonal arrays, reducing the number of sites for reactions with fixatives such as osmium tetroxide or tannic acid and thus resulting in negative staining (Niklas *et al.*, 1985). Senescence, detachment or other types of trauma may also produce negative staining; however, the chloroplast ultrastructure evident in the Clarkia samples does not typically survive senescence (Niklas *et al.*, 1985).

During senescence, or after any treatment resulting in the production of free radicals, the long-chain neutral lipid products of lipid peroxidation mediated by free radicals initiate the transformation of the membrane lipids from a liquid-crystalline phase to a hexagonally ordered gel phase (Thompson *et al.*, 1983). The presence of both phases increases the permeability of the membrane (Thompson *et al.*, 1983), but as mentioned above, decreases the number of sites for reaction during fixation and staining. It is of note that chilling can also produce this phase change (Thompson *et al.*, 1983; Bishop, 1983); senescence or trauma-induced processes effectively increase the temperature at which the transition will occur. In ultrathin leaf sections, intact chloroplasts of living *M. glyptostroboides* that had been detached and refrigerated at 6°C for an extended period also exhibited negative staining of the thylakoids membranes.

Additionally, in preparations of extracted chloroplasts, isolated from ground tissue by differential and density gradient centrifugation, negative staining of thylakoid membranes is observed in intact chloroplasts, while in broken chloroplasts in which the cell wall has ruptured releasing the soluble stroma, the isolated thylakoids stain positively (Hoober, 1984). This would seem to indicate that the production of free radicals as the result of stress, whether due to dehydration, osmotic shock or aging, originates in the stroma of the chloroplast, as opposed to on or within the membranes or in the cytoplasm of the cell. This is also supported by the observation that in very well preserved fossil chloroplasts, while the thylakoid membranes and lipid droplets are consistently electron lucent, the centers of lipid droplets frequently have a small electron dense area at the center (Figure 7-2), suggesting that the transformation originates at the surface of the droplet in contact with the stroma and progresses toward the core.

6. QUANTITATIVE ANALYSIS OF CHLOROPLAST PRESERVATION

Table 7-1 lists the chloroplast features that were assessed for the fossil leaflets and the percentage of samples in which their presence was observed. The features are arranged such that those at the top of the table represent the highest fidelity to the living state in terms of comparison to chloroplasts in living leaf samples, whereas those at the bottom represent the least.

Chloroplasts were characterized as *intact and exhibiting discernible thylakoid geometry* (Figure 7-7) if the quality of preservation was sufficient to allow the determination of the number of thylakoids per granum, the degree of grana stacking and the width of grana stacks. Additionally, the general shape of the individual chloroplast must have been evident; that is to say, the stroma-grana thylakoid system must be segregated in an obvious manner from its surroundings. In some cases, these ultrastructural characteristics were evident and clearly measurable, but were found in an area consisting of numerous closely spaced chloroplasts, packed such that the membranes separating the individual chloroplasts were not discernable.

Chloroplasts were described as being *intact and exhibiting evident ultrastructure* if the inner membrane system was evident throughout or in portions, but the quality of preservation was insufficient to allow the determination of the characteristics related to thylakoid geometry (Figure 7-8). *Stacked membranes* (Figure 7-7) were considered present in any area where there was a clear lamellar orientation to the internal membranes associated with the chloroplast. In the best case, the thylakoids were clearly the appressed members of a grana stack, but generally these membranes were likely to have been stromal thylakoids that became closely associated only after the vesiculation of the grana stacks, which allowed for the reduction of the gap between those the stromal thylakoids.

Chloroplast membranes were termed *associated* in any case where they were part of a clearly delineated organelle (Figure 7-9) and *disassociated* in

Table 7-1. Overall preservation quality in the fossil leaf tissues

Chloroplast features	Total number	Number of sections	Percentage of sections	Number of leaflets	Percentage of leaflets	Number of layers	Percentage of layers
Discernable Thylakoid Geometry	30+	14	13%	10	28%	6	50%
Evident Ultrastructure	80+	26	24%	15	42%	8	67%
Visible Stacked/Appressed Membranes (SM)	405	78	72%	35	97%	12	100%
Evidence of Displaced Starch Grains (ST)	127	46	43%	23	64%	11	92%
Associated Membranes (AM)	621	102	94%	36	100%	12	100%
Lipid Droplets (LD)	175	51	47%	25	69%	11	92%
Vesicular Membranes (VES)	157	58	54%	29	81%	11	92%
Disassociated Membranes (DM)	196	66	61%	31	86%	12	100%
Amorphous Breakdown Lipids (BDL)	767	106	98%	36	100%	12	100%
No Evidence of Chloroplast Related Structures	n/a	2	1.85%	0	0%	0	0%

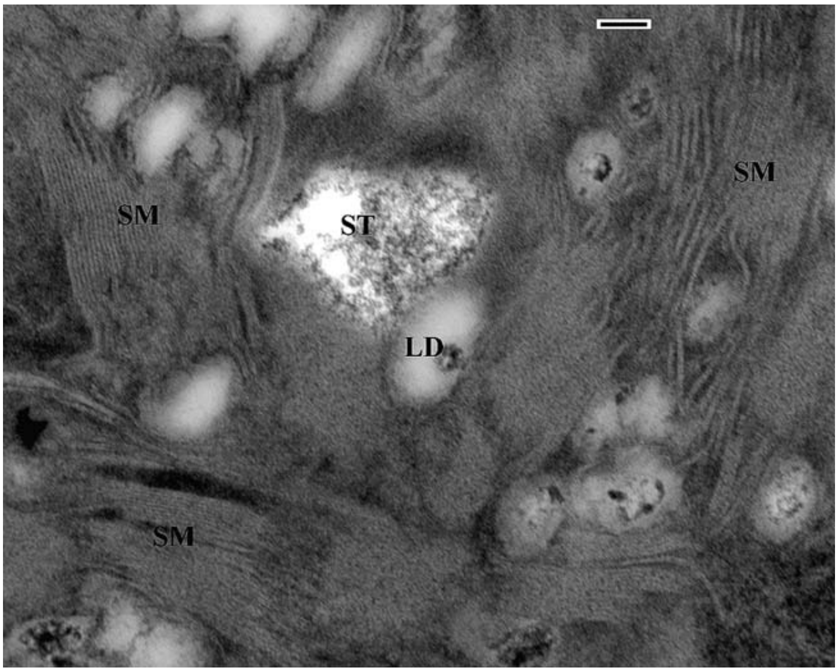

Figure 7-7. Grana stacks with evident geometry. Legend: Stacked membranes (SM); Lipid droplets (LD) and Starch remnants (ST). Scale bar = 100nm.

any case where they were randomly dispersed and could not be deemed part of any clearly delineated organelle (Figure 7-5).

Starch (Figure 7-10) was considered present when there was an area within a chloroplast body that appeared to have been occupied by a starch grain that had presumably decayed in place. Generally, the perimeter of such areas was demarcated with a thin outline of electron dense material, and the thylakoid membranes appeared to bend around it, as they would around a starch grain in the chloroplast of a fresh green leaf. In a few cases, material with the same appearance under TEM as an actual starch grain was observed.

Chloroplast membranes were termed *vesicular* (Figure 7-4) in any case where portions of either single double-membranes or stacks of membranes had broken off into vesicles—in cross section, small circular bodies with no contents. In many cases the stages of the vesiculation process were evident. *Lipid droplets* (Figure 7-10) were considered present when there were appropriately sized, electron lucent, rounded bodies evident, typically in close association with membranes. In the most highly preserved chloroplasts, these droplets typically displayed a small electron dense area near the center.

Breakdown lipids (Figure 7-9) were counted as present wherever there was an amorphous cloud of electron lucent material that by its size, shape

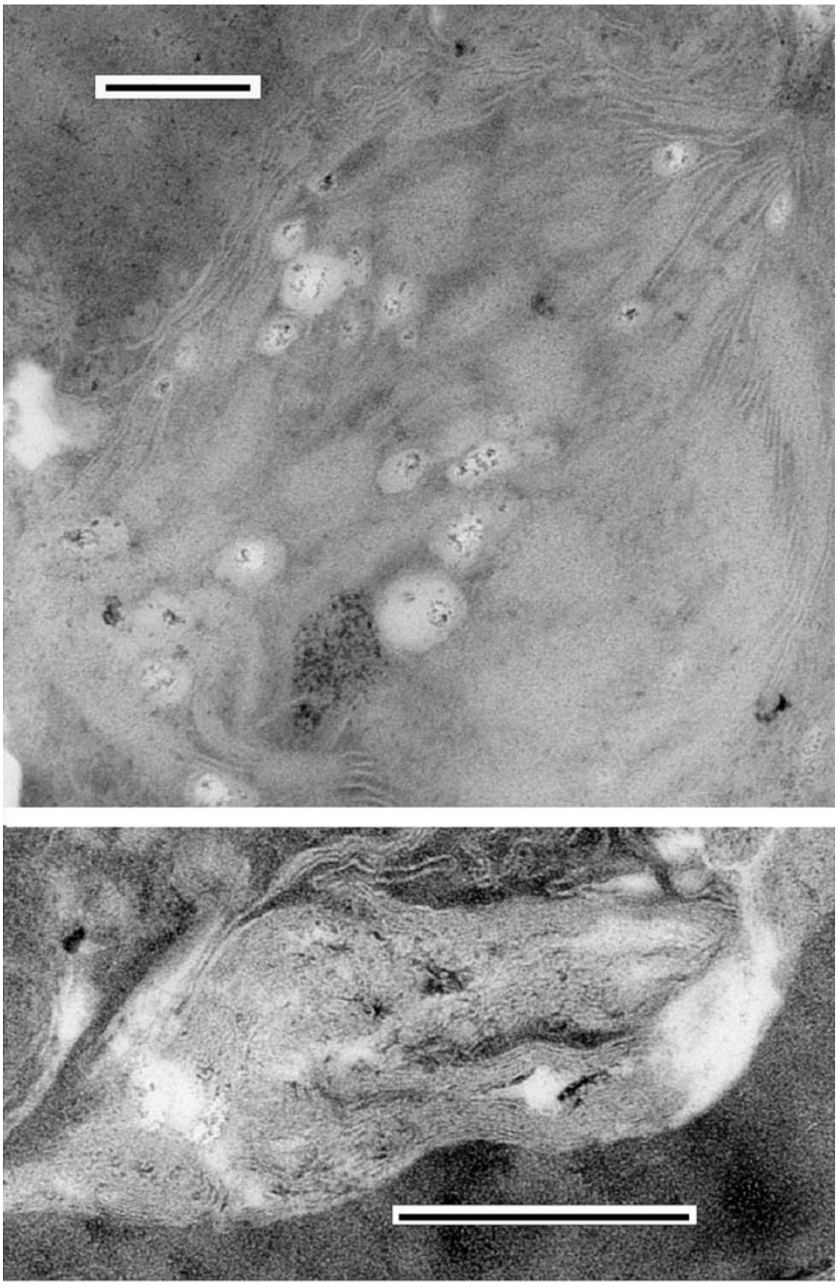

Figure 7-8. Intact fossil chloroplasts with evident ultrastructure. Note that although stacked membranes (SM) are obvious, the thylakoid features are not distinct enough to be measured. Scale bar = 500nm.

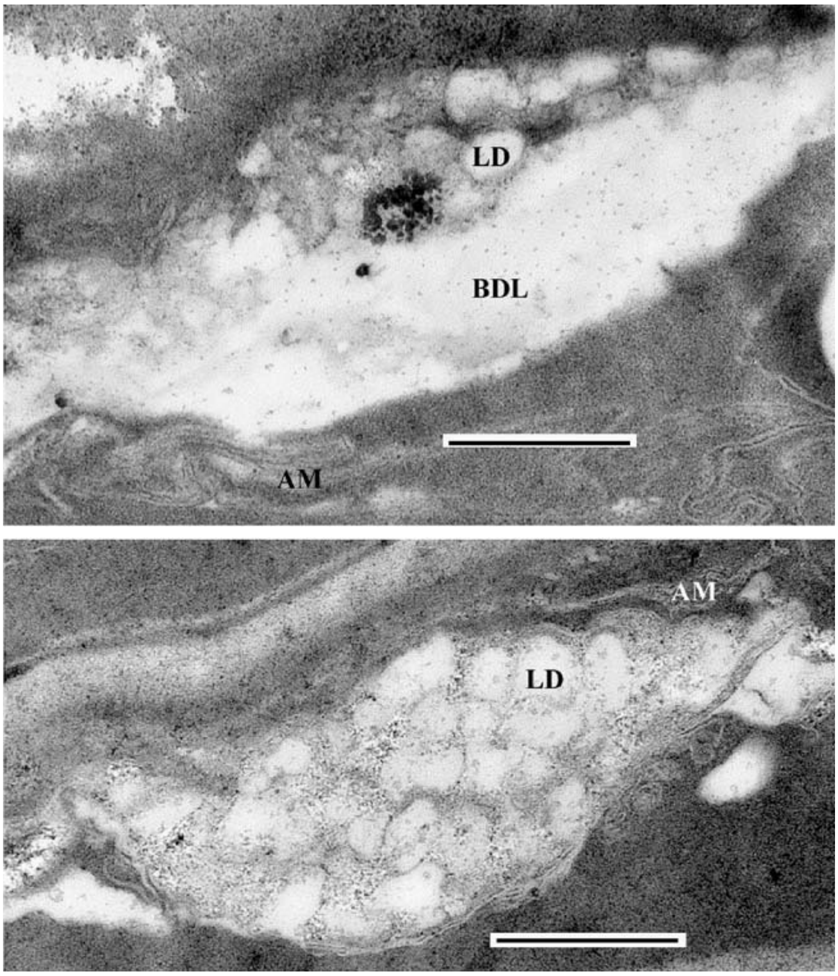

Figure 7-9. Associated membranes (AM). Fossil chloroplasts. Membranes are evident in association with lipid droplets and amorphous breakdown lipids (BDL). Scale bar = 500nm.

and association with chloroplast–scale membranes clearly was the result of the decomposition of those membranes. Intact chloroplasts were frequently encountered along the perimeter of large irregular bodies or bands of breakdown lipids. Additionally, portions of stacked membranes could often be discerned at the boundaries of those areas, as if some digestion process originating from the center of a cluster of chloroplasts had taken place.

Starch (Figure 7-10) was considered present when there was an area within a chloroplast body that appeared to have been occupied by a starch grain that had presumably decayed in place. Generally, the perimeter of such areas was demarcated with a thin outline of electron dense material, and the thylakoid

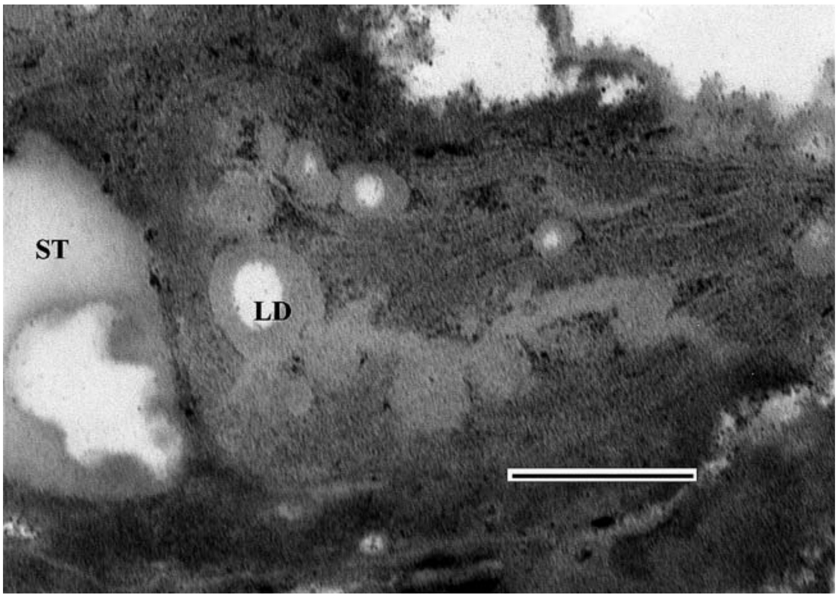

Figure 7-10. Chloroplast with intact grana stacks, lipid droplets (LD) and a large starch grain (ST) that has lost material at its center. Scale bar = 500nm.

membranes appeared to bend around it, as they would around a starch grain in the chloroplast of living leaves. In a few cases, material with the same appearance under TEM as an actual starch grain was observed.

Chloroplast membranes were termed *vesicular* (Figure 7-4) in any case where portions of either single double-membranes or stacks of membranes had broken off into vesicles; in cross section, small circular bodies with no contents. In many cases the stages of the vesiculation process were evident. *Lipid droplets* (Figure 7-10) were considered present when there were appropriately sized, electron lucent, rounded bodies were evident and typically in close association with membranes. In the most highly preserved chloroplasts, these droplets typically displayed a small electron dense area near the center.

Breakdown lipids (Figure 7-9) were counted as being present wherever there was an amorphous cloud of electron lucent material that by its size, shape and association with chloroplast–scale membranes that clearly was the result of the decomposition of those membranes. Intact chloroplasts were frequently encountered along the perimeter of large irregular bodies or bands of breakdown lipids. Additionally, portions of stacked membranes could often be discerned at the boundaries of those areas, as if some digestion process originating from the center of a cluster of chloroplasts had taken place.

Intact chloroplasts were observed in 41.6% of the fossil leaves examined and in 66.6% of the 5 mm intervals. In 27.7% of the leaves, the chloroplasts

Table 7-2. Significance from one-way nested ANOVA for each feature

	P-values	
Feature	Location/layer effect	Leaflet effect
SM	0.0957	0.0006
AM	0.2379	0.0055
DM	0.8843	<.0001
ST	0.1981	0.0209
VES	0.0128	0.001
LD	0.0686	<.0001
BDL	0.4266	0.0124

were so well preserved that features related to thylakoid geometry (i.e., the degree of grana stacking, number of thylakoids per granum, stack width) were measurable. Stacked membranes were observed in 97% of the fossil leaflet samples. Only 1.85% of the leaflets lacked evidence of chloroplasts or related structures.

The number of times each chloroplast feature was present in a given leaflet section was used to test for significant differences between intervals in the litter sample and between individual leaflets. As set forth in Table 7-2, when each feature was considered separately, only the presence of vesicular membranes (VES) revealed a significant difference between intervals, while there was an evident significant difference between individual leaflets for each of the individual features by the univariate analyses. The between interval mean square was tested against the between leaflet (within interval) mean square while the between leaflet mean square was tested against the between section (within leaflet) mean square.

When the features were considered simultaneously in multivariate analyses, the difference between intervals was found to be significant (for a 5% Type I error), and the leaflet effect was found to be highly significant, as summarized in Table 7-3. An additional multivariate analysis was performed using only the three features whose least squares means best distinguished between intervals (Table 7-4). When only the presence of stacked membranes (SM), vesicular

Table 7-3. Significance from one-way MANOVA of all chloroplast features

	P-value	
TEST	Location/layer effect	Leaflet effect
Wilks' Lambda	0.0169	<.0001
Pillai's Trace	0.0243	<.0001
Hotelling-Lawley	0.0156	<.0001

Table 7-4. Significance from One-Way MANOVA of SM, VES and LD

	P-value	
TEST	Location/layer effect	Leaflet effect
Wilks' Lambda	0.0013	<.0001
Pillai's Trace	0.0012	<.0001
Hotelling-Lawley	0.0014	<.0001

membranes (VES) and lipid droplets (LD) were considered, both the interval effect and leaflet effect were found to be significant at the 1% Type 1 error.

The mean frequencies of the presence of these three chloroplast features—stacked membranes, lipid droplets and vesicular membranes—per vertical 5mm interval within the section of lignite were plotted (Figure 7-11), revealing an apparent oscillation in quality of preservation over time. As shown in Table 7-5, the length to width ratio of the chloroplasts present in the fossil leaflets was on average 2.96, which was found to be significantly different from that of a random sample of living *M. glyptostroboides* leaves. However, the standard deviations of the angles of orientation for the chloroplasts within a section, which was intended to detect whether the l/w ratio in the fossils was representative of the original geometry in the living state or a by-product of deformation induced by compression were found to vary similarly between the modern and fossil

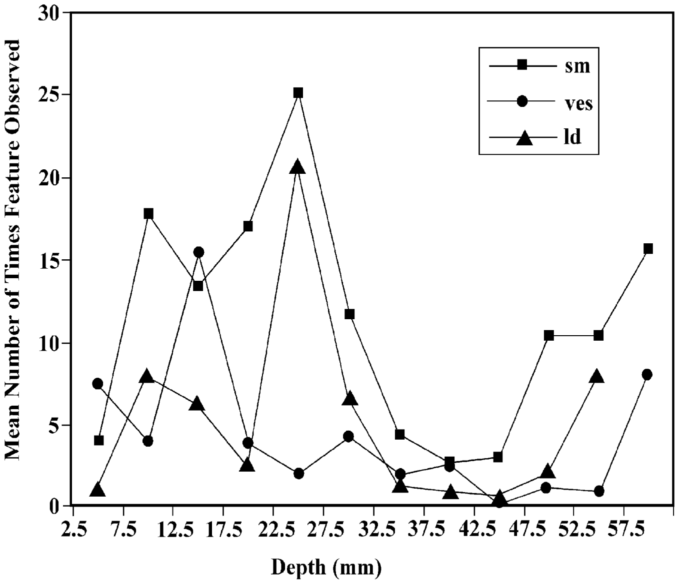

Figure 7-11. SM, VES and LD Presence Frequency versus Depth. Legend: sm = stacked membranes; ves = vesicles; ld = liqid droplets.

Table 7-5. Length to width ratios for chloroplasts in fossil and modern *Metasequoia* leaflets

	Ave. L:W	Min. L:W	Max. L:W	Ave. σ	Min. σ	Max. σ
Fossil	2.96	2.11	3.76	22.85	9.01	34.75
Living	2.47	1.90	3.10	21.06	14.93	32.80

samples such that there was no significant difference between the means for the two groups.

7. IMPLICATIONS OF QUANTITATIVE ANALYSIS

Since the fossil leaflet samples were derived from thick litter mats, presumably deposited over many hundreds of years by seasonal abscission of deciduous branchlets (cladoptosis), it was presumed that the leaflets would have undergone senescence prior to detachment of the branchlet, and would under conditions of optimum preservation, at best reflect the ultrastructural state characteristic of senescent leaves.

8. PATTERNS OF DEGRADATION: SENESCENCE VERSUS TRAUMA INDUCED DETACHMENT

A number of studies on the ultrastructural changes which take place within cells during leaf senescence have demonstrated a highly ordered pattern of degradation that is quite distinct from that observed in leaves that have been prematurely detached due to some sort of trauma. In a cell undergoing senescence or necrosis, the first detectable changes involve the loss of ER and Golgi body membranes, as well as a decrease in the number of ribosomes (Niklas *et al.*, 1985). The chloroplasts usually degenerate after the ER, although in some cases, they have been observed to be the last persisting organelle before the death of the cell (Niklas *et al.*, 1985; Hurkman, 1979). In senescing leaves, the internal chloroplast structure is completely dismantled; stroma proteins (RuBP carboxylase) and later chlorophyll are broken down, the thylakoid structures disappear and large plastoglobuli develop within the limits of the still intact double membrane bounding the organelle (Larcher, 1995). These globuli are believed to be formed from lipids produced during the disintegration of granal and stromal thylakoids (Burke *et al.*, 1984; Grover & Mohanty, 1993). The chloroplast is termed a gerontoplast at this point; having lost all chlorophyll and chlorophyll bearing structures, and the remaining globuli are essentially lipid droplets rich in carotenoid pigments. The gerontoplast loses its elliptical shape as the thylakoid system swells and the grana become vesicular, ultimately taking on a spherical form (Niklas *et al*., 1985). The external membrane itself is then finally degraded, signaling the death of the chloroplast (Hurkman, 1979; Grover & Mohanty, 1993). This typically occurs before the disappearance of the mitochondria or nuclei (Niklas *et al*., 1985).

It has been asserted that the envelope maintains its integrity so that the dismantlement of the chloroplast constituents can proceed in a controlled manner (Woolhouse, 1984). It is key to the process of senescence, whereby plants reclaim valuable nutrients from their leaves before shedding them, that the pigment complexes within the chloroplast are first dissociated by enzyme action breaking the porphyrin rings so that the harmless products, and most importantly, the nitrogen in the chlorophyll binding proteins, can be transported through the chloroplast envelope and into the vacuole. If these proteins were broken down first, then photodynamic chlorophyllides would be released into the cell, resulting in photo-oxidation and cellular death before the valuable nitrogen compounds could be withdrawn (Larcher, 1995). The nucleus is relatively stable during senescence/necrosis and its ultimate vesiculation and disappearance essentially mark the death of the cell (Niklas *et al*., 1985). In most cases, the mitochondria remain present through terminal necrosis, however they may demonstrate a reduction in size, swelling of the cristae and a reduction in number contemporaneous to the breakdown of chloroplasts (Niklas *et al*., 1985). A completely efficient process of senescence therefore leaves no organelles remaining within the cells of leaf tissues. Chloroplasts especially are removed early in breakdown procedure.

Alternatively, when green leaves are artificially detached or detached due to some trauma, the pattern of degeneration observed is quite different. In leaves that have been detached for several days, the membranes of the chloroplasts rupture, allowing their contents to spill into the cytoplasm. The thylakoid membranes, which remain associated with the other constituents of the chloroplast (lipid droplets, starch grains, etc.), persist long after the other organelles have disappeared (Larcher, 1995). This is consistent with observations made on isolated chloroplasts suspended in water or hypotonic buffer, in which the envelope swells and ruptures, liberating the contents of the stroma into the medium; the thylakoid system remains in one piece and osmiophilic globuli also tend to remain (Kirk & Tilney-Bassett, 1978). Under these circumstances, the remnants of the ruptured chloroplast envelope form numerous vesicles (Cline, 1985).

The observed preferential preservation of chloroplasts and chloroplast components cannot be identified with the pattern of degradation produced by senescence, as would have been expected, but it seems to be more consistent with that observed in leaves detached prematurely due to some trauma.

The presence of intact grana and stacked membranes is inconsistent with the observed effects of senescence on chloroplast ultrastructure, as is the elliptical shape of the chloroplasts. Although the test for shape is in a sense redundant where thylakoid membranes are easily identified as present in that the elliptical form of the chloroplast is maintained by the presence of that system of parallel, elongated membranes. Nonetheless, as there was no significant difference in the measure of random orientation between the fossil chloroplasts and equivalent modern samples, the elliptical shape cannot be attributed to compression alone, supporting the ultrastructural evidence that the plastids were not gerontoplasts. The significant difference between the means of the length to width ratios between the fossil and living samples may be attributed to the effects of post-depositional dehydration, which with an intact, parallel thylakoid system in place, would somewhat reduce the width, but not the length of the fossil chloroplast. This would result in the measurement of the length and width of the released thylakoid system, which would be narrower than the chloroplast as a whole, since starch grains and the stroma extend the envelope in the direction perpendicular to the thylakoids. The presence of vesicular membranes is also consistent with the effects of detachment rather than senescence.

It is crucial to note however, that studies on leaf senescence and aging have been conducted almost exclusively on angiosperms, as the deciduous habit is relatively rare among gymnosperms, and that the pattern of degradation observed during senescence may be significantly different for a deciduous conifer such as *M. glyptostroboides* or the middle Eocene *Metasequoia* of the Canadian High Arctic. This discrepancy has prompted an investigation into the ultrastructural changes observed specifically in deciduous conifers during autumnal senescence; preliminary observations made on senescent leaflets of *M. glyptostroboides* indicate that elliptical, starch-bearing chloroplasts with intact thylakoid geometry regularly persist, even when nuclei have also remained intact within a given cell, and that the endoplasmic reticulum also persists quite commonly, although mitochondria do not appear to be present. This apparent inefficiency of the senescence process for the speceis would explain the presence of chloroplasts in the fossil leaflets, though not their preferential preservation over the other persistent sub-cellular features.

It is possible that the highly organized internal structure of the chloroplast and tendency for the membranes to stain negatively, thus rendering them readily apparent, increased the probability that the organelle or its constituents would be identified even in an advanced state of degradation. The abundance of chloroplasts in contrast to nuclei would also contribute to this bias. However, there is substantial evidence that the post-depositional conditions favored chloroplast preservation, as certain circumstances that would preserve leaf tissue in general from fungal and bacterial attack would also prevent the decomposition of the chloroplasts in particular.

9. MECHANISM OF PRESERVATION

Noting that taxa characterized by high, naturally occurring concentrations of tannic acids were frequently found in the best state of preservation, Niklas *et al.* (1985) attributed the excellent ultrastructural preservation observed in the Clarkia leaf compressions to an "auto-fixation" process whereby dehydrated leaves were submerged in standing waters that were rich in tannic acid, presumably leached from the bark of partially immersed trunks and roots. Alternatively, in a dry environment, the proposed mechanism was the rupturing of tonoplasts containing high concentrations of phenolic compounds, resulting in the infiltration of the cells and their subsequent fixation. Additionally, it was reported that after dehydration and tannic acid fixation, chloroplast membranes appeared to be more stable than those of the nuclei or mitochondria (Niklas *et al.*, 1985), a finding consistent with the observed preferential preservation of chloroplasts in the Clarkia samples.

In a study of peats of Southern Florida, Cohen & Spackman (1977) reported a high frequency of tanniferous cell fillings in tree-dominated, autochthonous peats and attributed the preferential preservation of *Rhizophora* L. leaves to *Avicennia* L. leaves occurring within certain peat deposits to the presence of such tannin-like cell inclusions which were lacking in the latter. It was also noted that no staining was required in preparing the peat samples for light microscopy, as the samples had acquired a "natural stain."

In accordance, the mechanism proposed for the pristine preservation in peat deposits of leaves, exhibiting no evidence of cellular catabolysis, skeletonization or fungal penetration, was the accumulation in standing acidic (peat) water, as highly acidic waters would arrest or retard degradation, as well as inhibit fungal and bacterial growth (Cohen & Spackman, 1977; Gastaldo & Staub, 1999). Modern peats with high leaf frequencies and low matrix tend to accumulate in environments where the pH ranges from 3.6 to 4.1 (Cohen & Spackman, 1977; Gastaldo & Staub, 1999).

The presence of bacteria on and within the epidermis of the fossil leaflets indicates that the depositional environment was not necessarily hostile to these microbes in terms of oxygen availability, temperature or pH. However, the inefficacy of the bacteria in decomposing the leaf tissues implies that the tissues themselves may not have been amenable to the microbes, perhaps due to the abundance of tannins. This is supported by the observation that the bacterial cells present in association with the fossil leaves were generally of minimal diameter (<0.5 μm), characteristic of starved bacteria, which may exhibit diameters as little as 0.2 μm (Characklis *et al.*, 1990). Additionally, extracellular polysaccharide substances, the abundance of which is indicative of carbon availability to the bacteria in a biofilm (Lünsdorf *et al.*, 2000), were distributed relatively sparsely amid the clay particles encrusting the fossil leaves. The mineralized biofilm itself may also have contributed to the preservation of the leaflets.

The lower (inner) layers of a biofilm may frequently be limited by oxygen (Wardell *et al.*, 1980), such that it would not be unusual for anoxic conditions to prevail within a leaf that has been coated with a thick film. As the age and thickness of a biofilm increases, its diffusion coefficient decreases (Christensen & Characklis, 1990), such that the movement of substances into and out of the leaf would be constrained by the presence of the film. Biofilms may also influence the transport of heat due to their relatively low thermal conductivity (Christensen & Characklis, 1990), insulating the substratum to some degree and thus conferring protection against breakdown processes accelerated by heat. The incorporation of insoluble inorganics such as suspended particulates into biofilms influences the capacity of the film to immobilize water (Christensen & Characklis, 1990); clay particles, with their relatively high capacity to adsorb water, would therefore increase the capacity of the biofilm as a thermal insulator. The mineral-rich film would also provide physical protection against other microbial decomposers, as observed by Lünsdorf *et al.* (2000).

The significant variation in the state of preservation of chloroplasts between leaflets may reflect differences in the time required for a natural fixation process to occur, during which the degradation characteristic of detachment would proceed. The variation observed between the 5 mm intervals, which are considerably time-averaged such that leaflets from the same layer within the litter mat were not necessarily deposited during the same shedding event, may reflect fairly long term changes in the depositional conditions, which may have influenced the leaflets shed over a number of years or may in fact be the product of small-scale differences in diagenetic conditions. The oscillation in preservation quality, shown in Figure 7-11, appears to have a period of approximately 50 mm, with about 22.5 mm exhibiting above average preservation and 27.5 mm exhibiting below average reservation, although obviously a larger data set would be required to determine whether this pattern is actually perpetuated throughout the lignite layers. Relatively small-scale temporal variations in these deposits have previously been observed (Greenwood & Basinger, 1994). Using an estimate of the leaf lignite accumulation rate of 0.8mm/year (Kojima *et al.*, 1998), the period of the observed oscillation in terms of section thickness can be considered equivalent to approximately 62.5 years.

More specific information as to post-depositional conditions may yet be obtained from a study underway on the effect of pH, oxygen availability and temperature on the ultrastructural preservation in decaying litter of *M. glyptostroboides*; however, it is clear that fairly short term (<100 years) changes in paleo-environmental conditions may be detected from differences in the quality of preservation over a vertical gradient.

10. SUN/SHADE CLASSIFICATION OF FOSSIL LEAFLETS

There are a number of leaf characteristics that are sensitive to the intensity of incident light. On an ultrastructural scale, characteristics of the chloroplast such as the number of thylakoids per chloroplast section, width of grana stacks, number of thylakoids per granum, degree of stacking, size of starch grains and abundance of plastoglobuli also differ with light environment (Lichtenthaler & Meier, 1984). It is of note, however, that the sensitivity of these features generally has been observed in angiosperms; anatomical and morphological responses to incident light intensity have not been as extensively studied for gymnosperm taxa (Arens, 1997).

Although not all of the characteristics mentioned may be preserved in fossil leaf tissues, a limited number of studies have used specific features in fossils to interpret the original light environment to which the living leaf was subject. Guignard *et al.* (2001) examined cuticle ultrastructure via TEM to classify samples of the Jurassic pteridosperm *Komlopteris nordenskioeldii* (Nathorst) Barbacka as having originated in sun or shade environments based on cuticle thickness and the presence of electron lucent amorphous material, granular regions and fibrous elements, substantiated by observations on stomatal apparatus and pinnule area. Arens (1997) used anatomical features preserved in fossil specimens, such as segment thickness, cuticle thickness, stomatal appearance, palisade characteristics and the presence of papillae or hairs to classify several common *Alethopteris* Sternberg and *Neuropteris* (Brongniart) Sternberg taxa as displaying "sun-type" morphology. No such investigation on fossil chloroplast ultrastructure has been conducted, no doubt due to the rarity of adequate preservation.

There are also chemical differences between sun and shade type leaves, such as chlorophyll concentration, the ratio of chlorophyll a to b, the ratios of specific carotenoids (Larcher, 1995; Lichtenthaler & Meier, 1984) and the concentration of manganese (McCain & Markley, 1989). It has been reported that the concentration of leaf pigments in modern *M. glyptostroboides*, among other taxodiaceous conifers, responds to shading, with chlorophyll and carotenoid contents increasing with decreasing light intensity (Ida, 1981). Given the relationship between thylakoid structure and chlorophyll content, this suggests that there should be an analogous ultrastructural response to light environment.

10.1. Results of Sun/Shade Classification Analysis

Of the thirty-six fossil leaflets examined, only nine demonstrated preservation of ultrastructural chloroplast features adequate for the purpose of

Table 7-6. Measurements of ultrastructural chloroplast features of fossil leaflefts

Location	Leaf #	Section #	Thylakoids per stack		Grana per stack		Thylakoids per granum		Stack width (nm)
			min.	max.	min.	max.	min.	Max.	
10–15mm	1	3	4	24	2	7	2	4	296
10–15mm	2	1	2	4	1	2	1	2	207
10–15mm	2	1	4	10	2	5	1	3	232
10–15mm	3	1	10	38	5	10	2	4	415
10–15mm	3	1	8	11	4	5	2	4	354
15–20mm	2	1	1	2	1	2	1	2	None
15–20mm	2	1	2	8	1	4	2	3	215
15–20mm	2	3	1	1	1	1	1	1	None
25–30mm	1	1	4	19	2	7	2	4	306
25–30mm	1	3	6	10	3	4	2	5	369
25–30mm	1	3	4	22	2	6	2	6	420
25–30mm	2	1	6	36	3	12	2	4	363
25–30mm	2	1	4	33	2	8	2	4	329
25–30mm	2	1	10	25	4	8	2	5	387
25–30mm	2	2	10	30	4	10	2	5	343
25–30mm	2	2	6	36	2	12	2	4	400
25–30mm	2	3	4	21	2	7	2	4	360
25–30mm	2	3	5	17	2	8	2	4	313
25–30mm	2	3	4	24	2	8	2	4	331
25–30mm	2	3	5	15	3	6	2	4	312
25–30mm	2	3	6	25	3	8	2	4	330
25–30mm	2	3	8	38	3	9	2	5	375
25–30mm	2	3	8	20	3	10	2	3	295
25–30mm	3	2	8	15	3	5	2	4	311
30–35mm	3	1	1	10	1	6	1	3	319
40–45mm	1	1	7	16	2	5	2	4	364

measurement. In some of the leaflets, multiple chloroplasts from more than one section were sufficiently preserved, while in others, only a single chloroplast was acceptable for examination. The measurements recorded for each chloroplast are shown in Table 7-6. The column labeled ‘location’ denotes the layer along the vertical gradient in the section of lignite from which the leaflet was extracted.

The “sun-type” and “shade-type” values for the ultrastructural features of interest, established from a study on modern *M. glyptostroboides*, are listed in Table 7-7. The values for the shade leaves are generally higher than those for the sun-type leaves, and in many cases more than double. The source data from which these means were calculated were also used to create the dispersion matrix employed in the classification analysis. Four different analyses were performed using different combinations of the ultrastructural features measured. The chi-square values resulting from these analyses, as well as the group

Table 7-7. Means for sun and shade groups in *Metasequoia glyptostroboides* (October)

	Min. no. thylakoids per stack	Max. no. thylakoids per stack	Min. no. grana per stack	Max. no. grana per stack	Min. no. thylakoids /granum	Max. no. thylakoids /granum	Ave. stack width
Sun	5	21	2	7	2	4	510 nm
Shade	2	10	1	3	1	3	401 nm

assignments based on those values, are listed in Table 7-8. It is clear that in many cases, the results of the various analyses conflicted. In making final assignments of type, consideration was given to how strongly the chi-square values differed by the various methods of analysis. A summary of the final classification results by leaflet is shown in Table 7-9. The leaflets appeared to be fairly evenly distributed between sun and shade types, as five of the nine were identified as being sun-type.

10.2. Discussion of Sun/Shade Classification

An interesting feature of the classification analysis of the fossil leaflets is that for most of the samples, the ultrastructural features relating to the degree of thylakoid and grana stacking were characteristic of the "shade-type" arrangement, while the grana stack widths were more indicative of the "sun-type" geometry. In fact, if stack width alone was used to evaluate the fossil leaflets, all nine would be classified as "sun-type". This discrepancy may relate to the influence of light quality and/or light regime. It was suspected that the features might vary from the beginning to the end of the growing season, but this concern was addressed by comparing modern sun and shade leaflets sampled in early May to those sampled in October.

Thylakoid geometry is influenced not only by the intensity of the light incident upon the leaf surface, but also by the spectral quality of the irradiance. For example, exposure to blue light ($\lambda_{\max} = 450$ nm) versus red light ($\lambda_{\max} = 660$ nm) alone yields differences in ultrastructural features such as the degree of stacking and the stack width similar to those observed for high versus low light intensities of the same spectral distribution (Lichtenthaler & Meier, 1984). The percent relative distribution of solar radiation between high and low wavelength spectral intervals varies with latitude such that at higher latitudes, shorter wavelengths are attenuated. For example, whereas the relative spectral quality of incident light at 38° latitude is 33% short wavelength (290–617nm) and 67% long wavelength (617–3000nm), at 73.3° latitude only 20% is short wavelength (Kondratyev, 1969) at the same solar height. This difference in light quality, rather than intensity may partly have influenced the characteristics observed in the fossil *M. glyptostroboides* leaflets, as the relative enrichment of the light in longer wavelengths (red through infrared) would have promoted

Table 7-8. Assignment of fossil leaflets as “Sun” or “Shade” type based on minimum chi-square rule

		1			2			3			4			
Layer	Leaf	Shade χ^2	Sun χ^2		Shade χ^2	Sun χ^2		Shade χ^2	Sun χ^2		Shade χ^2	Sun χ^2	Group (4)	Final
10–15mm	1	97	800	shade	1485	2131	Shade	97	85	sun	88	1561	shade	**Shade**
10–15mm	2	2668	568	sun	303	244	Sun	2086	1015	sun	5904	1398	sun	
10–15mm	2	11871	6720	sun	3261	2514	Sun	5427	3819	sun	11466	4597	sun	**Sun**
10–15mm	3	613	1320	shade	585	1242	Shade	5726	7490	shade	6303	13895	shade	
10–15mm	3	14154	9005	sun	8045	7437	Sun	4044	2778	sun	3594	548	sun	**Shade**
15–20mm	2	n/a	n/a	n/a	911	305	Sun	10096	7722	sun	n/a	n/a	n/a	
15–20mm	2	1863	396	Sun	331	572	Shade	5255	3656	sun	4756	1018	sun	
15–20mm	2	n/a	n/a	n/a	692	520	Sun	4699	2990	sun	n/a	n/a	n/a	**Sun**
25–30mm	1	2022	495	sun	69	168	Shade	2180	1277	sun	1856	104	sun	
25–30mm	1	9263	5226	sun	4870	4413	Sun	4874	3556	sun	4370	875	sun	
25–30mm	1	409	328	sun	59	286	Shade	509	354	sun	356	626	shade	**sun**
25–30mm	2	652	283	sun	107	377	Shade	78	314	shade	118	2199	Shade	
25–30mm	2	3886	7922	shade	9133	10468	Shade	3639	5002	shade	4102	10439	shade	
25–30mm	2	3057	1757	sun	1180	1625	Shade	533	264	sun	374	480	shade	
25-30mm	2	3963	2169	sun	1137	1538	Shade	1008	558	sun	783	220	sun	
25–30mm	2	1585	4679	shade	3581	4718	Shade	163	565	shade	255	2883	shade	
25–30mm	2	327	274	sun	167	485	Shade	377	90	sun	259	656	shade	
25–30mm	2	4883	2161	sun	1087	1000	Sun	7204	5497	sun	6590	1897	sun	
25–30mm	2	381	244	sun	291	642	Shade	432	118	sun	305	601	shade	
25–30mm	2	9714	5339	sun	3798	3216	Sun	3423	2257	sun	3010	345	sun	
25–30mm	2	1523	462	sun	80	328	Shade	174	42	sun	111	1067	shade	
25–30mm	2	4878	9703	shade	8867	10649	Shade	4613	6266	shade	5126	12129	shade	
25–30mm	2	7242	3975	sun	2039	2053	Shade	7092	5338	sun	6493	1858	sun	**shade**
25–30mm	3	1683	1058	sun	279	976	Shade	1367	657	sun	1120	136	sun	**sun**
30–35mm	3	10231	5286	sun	4461	3302	Sun	6255	4577	sun	12705	5428	sun	**sun**
40–45mm	1	1018	3628	shade	3030	4375	Shade	348	63	sun	240	715	shade	**shade**

Table 7-9. Summary of Sun/Shade classification

Total number of leaflets examined	36
Number of leaflets with measurable thylakoid features	9
Number of leaflets classified as "sun-type"	5
Number of leaflets classified as "shade-type"	4

the development of "shade-type" features. A specific investigation into the effects of a 10–15% change in light quality on thylakoid development would be necessary to determine the extent of the influence of this factor. Aside from spectral distribution, the light regime characteristic of the Arctic, constant daylight from April through August and perpetual night by late November may also have influenced the thylakoid features observed in the fossil chloroplasts. Again it would require a specific investigation to determine the relationship between the influences of duration of exposure and light intensity on chloroplast ultrastructure.

The variation of the light sensitive ultrastructural features examined over the course of the growing season in modern *M. glyptostroboides* proved to be significant; however, based on the significance of the interaction between light environment and sampling month, this may largely have been due to the waning quantity of incident light associated with the onset of autumn. The sun leaves appeared to be more strongly influenced by this effect than the shade leaves, as evinced by the comparison of the means for the two groups in May versus October. Additionally, the differences between the sun and shade means were less distinct at the end of the growing season than at the beginning. Accordingly, the classification analysis of the fossil samples used only data from the leaflets sampled in early October for the sun and shade group means and the construction of the dispersion matrix, since the leaflets in the ancient litter mats presumably were deposited at the end of the growing season as the result of autumnal senescence. As an aside, these results contrast interestingly with the observation of Lichtenthaler & Meier (1984), who found that measurements of certain thylakoid features in shade leaves taken in May and between June and October differed, although the measurements in sun leaves remained fairly constant throughout the season. At the end of the season, the differences in the means for some thylakoid characteristics between sun and shade leaves were more distinct than at the beginning.

Additionally, there may be a taphonomic bias favoring the preservation quality of chloroplasts exhibiting high as opposed to low degrees of stacking. "Sun-type" chloroplasts frequently consist of primarily unstacked stromal thylakoids. Even when the chloroplast envelope ruptures, releasing its contents into the cell, the thylakoid system tends to remain intact (Larcher, 1995; Kirk & Tilney-Bassett, 1978). As grana stacks serve to connect disparate stromal lamellae, their presence may promote the persistence of the thylakoid system's integrity after the external double membrane has been destroyed. Thus "shade-type" chloroplasts may be more likely to be preserved in a readily recognizable state than "sun-type". Conversely, the senescence-related dismantlement of chloroplast ultrastructure, during which thylakoid stacks dissolve, would tend to produce a bias in favor of the misidentification of chloroplasts as "sun-type" in cases where senescence had been initiated, but not completed.

A final, yet nonetheless very important concern involves the random variation between individual chloroplasts within a given leaflet. As this variation appears to be greater than the random variation between leaflets exposed to similar light environments, the classification of unknown leaf samples as sun or shade-types will be more accurate if the average values per leaflet, based on at least 10 chloroplasts, are used rather than measurements of individual chloroplasts. When the classification analyses were performed on modern samples as a test, the classification based on the average of 10 chloroplasts per leaf was correct for 100% of the samples, however when each chloroplast was classified as sun or shade separately, the identification was incorrect for 10–40% of the samples depending on the combination of features used in the analysis, with the tendency towards misidentifying shade samples as sun types. This significantly increases the difficulty of assessing fossil leaflets due to the limited presence of chloroplasts within the ancient samples, yet must be taken into consideration in order for the classification to be performed with confidence.

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Chapter 8

Biomolecules from Living and Fossil *Metasequoia*: Biological and Geological Applications

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Abstract: Biomolecules from living and fossil *Metasequoia* Miki provide insight into the biological and geological history of the genus, as well as its phylogeny and evolution, population

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structure and molecular taphonomy. Chemically labile biomolecules such as protein and nucleotide sequences from *Metasequoia glyptostroboides* Hu *et* Cheng have reconfirmed the systematic position of *Metasequoia* as the sister taxon to *Sequoia* Endlicher and *Sequoiadendron* J. Buchholz. These three genera form the subfamily Sequoioideae, which is one of the basal groups of the Taxodiaceae-Cupressaceae complex. Relative rate testing based on different gene sequences suggests an evolutionary rate slow down in the Sequoioideae lineage. Non-sequence based molecular studies indicate a low overall genetic diversity and a lack of spatial genetic structure in its native population in southern China. An isolated tree in Paomu, Hunan Province was found to contain both molecular and morphological plesiomorphic characteristics, providing important clues to its evolutionary history. Moreover, given the importance of these data, critical conservation issues are raised regarding the management and preservation of the genus. Molecular and biochemical investigations of ancient biomolecules from well-preserved Tertiary fossil *Metasequoia* remains reveal the preservation of labile biomolecules such as carbohydrates that are normally absent from the Cenozoic fossil record. Comparative geochemical and SEM analyses of well preserved fossil specimens revealed the sources of these chemically unstable biomolecules and suggests that they may carry important structural functions to support the integrity of plant fossil morphology. These ancient biomolecules from fossil *Metasequoia* also offer valuable information regarding the environmental factors controlling the preservation of labile biomolecules and possible origins of homologous series of *n*-alk-1-ene/*n*-alkane pairs preserved in the geological record.

Key words: conservation; Cupressaceae; DNA; evolution; lignin, molecular phylogeny; Napartulik; Paomu; Shui-sha-ba Valley; Taxodiaceae.

1. INTRODUCTION

Several unique characteristics of *Metasequoia* Miki made this plant genus an interesting candidate for molecular level investigations, targeting on various evolutionary biology and geological questions. Its long, widespread and well-documented fossil record offers a continuous evolutionary history of morphological and biogeographic changes over the past 100 million years (Ma) (Yang & Jin, 2000; LePage *et al.*, this volume; Meyer, this volume; Momohara, this volume). The lack of significant morphological change since the Cretaceous suggests that *Metasequoia* is evolutionarily static; however, the mechanism(s) responsible for such evolutionary conservation has yet to be revealed at the molecular level. Previous morphological and anatomical studies on *Metasequoia* have laid a solid foundation for biomolecular investigations and generated new questions that are ripe for further molecular-level testing. For living *Metasequoia glyptostroboides* Hu *et* Cheng, the molecular genetic information will likely provide insight into the conditions and dynamics of its restricted distribution and might subsequently yield critical information to aid in the management and conservation of the genus. On the other hand, extraordinarily well-preserved fossil *Metasequoia* will provide exciting opportunities to explore its paleobiology through geological time.

Since the discovery of living *M. glyptostroboides* in southern China in the early 1940s, the rapid advancement of molecular and biogeochemical technologies have permitted a better understanding of the biology, genetics and physiology of this genus. Hypotheses and ideas that were initially proposed on the basis of morphological observations and anatomical comparisons were independently tested using various molecular techniques. When the preservation of *Metasequoia* fossils permitted it, techniques used to analyze living materials were applied to fossil remains. Such molecular investigations on both extent and extinct *Metasequoia* have offered exciting platforms for collaborations among molecular biologists, geochemists and neo- and paleobotanists. These interdisciplinary interactions have a great impact on our understanding of the genus both in the present and the geologic past.

This chapter provides a synthesis of previous molecular work on living and fossil *Metasequoia*. The types of biomolecules and techniques employed are outlined prior to the discussion of the various biological and geological applications. Whereas different molecular and geochemical methods are used to characterize the biomolecules from *Metasequoia*, modern DNA sequence data are widely applied for the reconstruction of phylogenetic trees and the calculation of evolutionary rates. Non-sequence data derived from studies of nucleic acids are used for population genetic evaluation. New results on biomolecules from Tertiary fossil *Metasequoia* are discussed to address questions regarding fossil preservation. Chemically stable biomolecules, such as structural biopolymers and lipids recovered from fossil remains, and their applications lead to a better understanding of molecular taphonomy, the origin of specific biomarkers in sediments, and paleoclimatic and paleophysiological interpretations. Although this chapter attempts to provide a comprehensive review on the biomolecules of both modern and ancient *Metasequoia*, not every natural product from this genus is discussed in detail, especially those chemical extracts that are less relevant to geologic applications. Interested readers are referred to Enoki *et al.* (1977) for metasequirin and to Otto & Wilde (2001) for terpenoids.

2. BIOMOLECULES AND APPLIED TECHNOLOGY

A suite of biomolecules from living and fossil *Metasequoia* has been targeted for molecular level investigations by employing various molecular and biochemical analytical techniques. Table 8-1 summarizes these molecules and the pursued biological and geological questions. In general, biologically informative, but chemically unstable macrobiomolecules, such as DNA and proteins, are the molecules of choice for studying modern *Metasequoia* tissues.

Table 8-1. Biomolecules and molecular techniques applied to *Metasequoia*

Biomolecule	Technology	Tissue type	Targeted question	References
Hydrocarbon lipids	GC, GC-MS	Modern and ancient leaves	Molecular preservation, chemotaxonomy	Lockheart *et al.*, 2000, Yang, unpublished data.
Terpenoid lipids	GC, GC-MS	Modern cones	Molecular preservation, chemotaxonomy	Otto & Wilde, 2001.
Biopolymers	Py-GC-MS	Modern and ancient leaves and wood	Molecular preservation	Obst *et al.*, 1991; Yang, *et al.*, in press
Purified cellulose	IRMS	Modern and ancient wood	Paleoclimate	Jahren & Sternberg, 2002, 2003.
Proteins	RIA, HPLC	Modern leaves	Phylogeny, physiology	Price & Lowenstein, 1989; Hager & Wind, 1997; Yang *et al.,* 1999.
Genomic DNA	RAPD, AFLP	Modern leaves	Genetic diversity	Kuser *et al.*, 1997; Zhang & Li, 1994a, 1994b; Li *et al.*, 1999; Tsumura *et al.*, 1995; Li *et al.*, 2003a.
Nucleotide sequences	PCR, Sequencing	Modern leaves (Appendix A)	Phylogeny, genetic diversity	Brunsfeld *et al.*, 1994; Li & Yang, 2003a; Tsumura *et al.*, 1997; Gadek *et al.,* 2000; Kusumi *et al.*, 2000.

Legend: Py-GC-MS: pyrolysis-gas chromatography-mass spectrometry; GC-MS: gas chromatography-mass spectrometry; HPLC: high performance liquid chromatography; IRMS: isotope ratio mass spectrometer; PCR: polymerase chain reaction; RAPD: random amplification of polymorphic DNA; AFLP: amplification of fragment length polymorphism; RIA: radioimmunoassay.

The radioimmunoassay (RIA) technique and the high performance liquid chromatography (HPLC) are standard analytical tools for protein studies. The RIA method involves the use of radioactive labeled antibodies, which bind to tested protein antigens and provides phylogenetic information (Price & Lowenstein, 1989). The phylogenetic distances among taxa can be measured by comparing the intensities of RIA reactions between an antibody from a known taxon with protein antigens from several tested samples. A strong reaction reflects a close phylogenetic relationship. Alternatively, HPLC can separate different proteins by allowing a dissolved protein solution to pass through a column. The proteins in solution are purified so that amino acid sequence data can be obtained (Skoog *et al.*, 1998).

At the nucleic acid level, genomic DNA can be prepared for restriction enzyme analysis, which involves cleaving the target DNA using restriction endonucleases, which are enzymes that precisely cut the DNA in a predictable and reproducible manner (Olmstead & Palmer, 1994). Analysis of the cut DNA fragments allows for the detection of the genetic diversity in a population or the estimation of genetic distances among compared taxa. However, it was the development and application of the polymerase chain reaction (PCR) (Saiki *et al.*, 1988) that revolutionized the practice of molecular biology, including molecular systematics. PCR can randomly amplify genomic DNA that serves as the basis for random amplified polymorphic DNA (RAPD) analyses, a PCR-based technique that detects genetic variation at the population level (Williams *et al.*, 1990). Targeted gene sequences can be amplified through PCR by using primers designed to flank conservative regions of the targeted DNA sequences, and PCR generated products can be further sequenced to determine the arrangement of the nucleotide bases (Sanger *et al.*, 1977), which in turn provides molecular characters for phylogenetic analysis (Freeman & Herron 1998). Enzyme-digested DNA fragments can also be amplified through PCR, and the resulting fragments, known as amplified fragment length polymorphism (AFLP), can be used for genetic fingerprinting (Vos *et al.*, 1995).

With some rare exceptions, only chemically stable biomolecules such as lipids and lignin are preserved in the fossil record. Although they contain less biological information compared to DNA or proteins, these stable biomolecules and their isotopic signals may carry the signatures of their biological predecessors and the ancient environments under which these molecules were synthesized. Therefore, lignin and lipids are suitable subjects for paleomolecular studies of *Metasequoia* fossils.

Organic extraction can remove lipids (all substances that can be dissolved in organic solvents) from plant tissues, leaving insoluble organic residues that are largely composed of structural biopolymers in the form of framework macromolecules (Figure 8-1). Different lipid compounds can be further separated through gas chromatography (GC) and the fractionated compounds can then be identified using online gas chromatography—mass spectrometry (GC-MS) (Skoog *et al.*, 1998). The application of online pyrolysis-gas chromatography-mass spectrometry (Py-GC-MS) provides an effective means of evaluating molecular preservation, especially for structural biopolymers in plant fossils (Boon, 1991; van Bergen *et al.*, 1996; Stankiewicz *et al.*, 1998a; Briggs, 1999 and references therein). Using a minimal amount of fossil material, the original composition and structure of ancient biomolecules can be inferred from the analysis of pyrolysis products. The addition of chemical tetramethylammonium hydroxide (TMAH) improves the technique by increasing the sensitivity for the detection of fatty acids and preferentially shows them on a pyrogram (Grasset *et al.*, 2001).

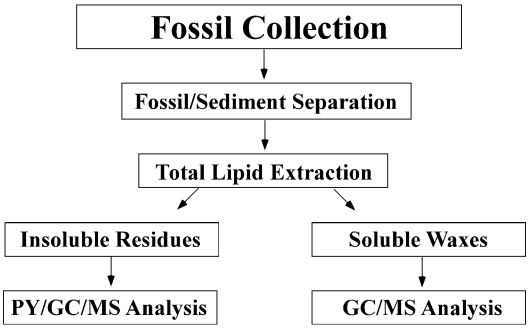


Figure 8-1. A flow chart of experimental procedures for the biochemical analysis of *Metasequoia* tissues.

In comparison with extracts from living *Metasequoia*, investigations of *in situ* biomolecules from *Metasequoia* fossil remains have focused on two remarkably well preserved Tertiary deposits: the Miocene Clarkia lacustrine beds in northern Idaho of the United States (15–16 Ma) (Smiley *et al.*, 1975; Smiley & Rember, 1985) and the Paleocene (∼60 Ma) and Eocene (∼45 Ma) floodplain deposits from the Canadian Arctic Islands (Christie & McMillan, 1991; McIver & Basinger, 1999). The islands of the Canadian Arctic Archipelago have yielded a number of plant fossil localities, some with three-dimensionally preserved fossils, including *Metasequoia* leaves, seeds, cones, and *in situ* stumps (Ricketts & Stephenson, 1994; Kalkreuth *et al.*, 1996). Obst *et al.* (1991) and Kalkreuth *et al.* (1996) performed some of the initial chemical characterizations of the wood. More recently, Jahren & Sternberg (2002, 2003) performed geochemical studies and Williams *et al.* (2003a, 2003b) reconstructed the stand structure, forest biomass and productivity of some middle Eocene (45 Ma) fossil forests from Napartulik, eastern Axel Heiberg Island. Molecular investigations on the preservation of the structural biopolymers preserved in the *Metasequoia* fossil leaves from Napartulik were recently conducted (Yang *et al.*, in press). In conjunction with SEM observations on the transverse sections of these fossil leaves, the results of these studies have revealed anatomical and molecular evidence for the taphonomy of these fossil deposits.

3. DNA AND PROTEINS FROM *METASEQUOIA GLYPTOSTROBOIDES*

3.1. Molecular Phylogeny and Evolution

Molecular studies have a major impact on our understanding of the phylogenetic position of *M. glyptostroboides*. Shortly after the discovery of

M. glyptostroboides Stebbins (1948) conducted a chromosomal analysis of the species and suggested that *M. glyptostroboides* ($2n = 22$) was more closely related to *Sequoiadendron* J. Buchholz ($2n = 22$) than to *Sequoia* Endlicher ($2n = 66$). However, later chromosomal studies (Schlarbaum *et al.*, 1983, 1984; Schlarbaum & Tsuchiya, 1984) on marker chromosome types indicated that the two California redwoods were more closely related to one another than either one of them was to *Metasequoia*. Nonetheless, despite the deciduous habit shared with *Taxodium* Richard and *Glyptostrobus* Endlicher, chromosomal studies supported a close affinity among *Metasequoia*, *Sequoia*, and *Sequoiadendron* as a natural clade within the family Taxodiaceae.

Early molecular attempts to affirm the systematic position of *Metasequoia* employed the use of immunological analysis of proteins (Price & Lowenstein, 1989). Their results confirmed the grouping of *Metasequoia* with the two North American redwood genera, which displayed the closest immunological distance with *Metasequoia*. Subsequent studies using modern DNA sequence data made large scale and multi-taxon comparisons possible, and the results quantitatively substantiated previous conclusions. Using chloroplast *rbc*L gene sequences, Brunsfeld *et al.* (1994) reconstructed a multi-taxon phylogeny of the Taxodiaceae and Cupressaceae. *Metasequoia* was found to be the sister taxon with *Sequoia* and *Sequoiadendron*, and this branch leading to the "sequoioid clade" has a very strong statistical support (bootstrap value of 100%). This phylogenetic arrangement was further supported by a later study using PRC-RFLP data of chloroplast genes (Tsumura *et al.*, 1995) and was reinforced by more recent analyses using other gene sequences from *mat*K, *chl*L and the *trn*L-*trn*F IGS region (either separated or combined datasets, Kusumi *et al.*, 2000) and 28S rDNA (Li & Yang, 2003b). This level of congruence achieved using extended DNA sequence length and different phylogenetic algorithms demonstrated the robustness of the phylogenetic reconstruction involving *Metasequoia*. These comparisons also indicated that the traditionally separated families, Cupressaceae and Taxodiaceae, form a monophyletic group (excluding *Sciadopitys*), justifying the morphological treatment of including the Taxodiaceae within the Cupressaceae (Eckenwalder, 1976). Using integrated molecular and morphological datasets, Gadek *et al.* (2000) adopted an intrafamilial classification for the Cupressaceae in which *Metasequoia*, *Sequoia* and *Sequoiadendron* are grouped within the subfamily Sequoioideae (see LePage *et al.*, this volume, for phylogenetic tree).

Comparison of nucleotide sequences between *Metasequoia* and related taxa in the Cupressaceae suggested relatively lower substitution rates in the Sequoioideae lineage. Kusumi *et al.* (2000) detected low substitution rates in the Taxodiaceae at both synonymous and non-synonymous sites in two chloroplast genes, and a similar observation was made on synonymous substitutions in several nuclear genes (Kusumi *et al.*, 2002). Furthermore, an evolutionary rate slow down was found in synonymous substitutions of 11 nuclear genes in the subfamily Sequoioideae relative to the Taxodioideae and Cupressoideae (Kusumi *et al.*, 2002). The low nucleotide substitution rates in the Taxodiaceae were also detected by comparing *rbc*L sequences from living and fossil *Taxodium*, a deciduous taxodiaceous conifer that is closely related to *Metasequoia* (Soltis *et al.*, 1992). Using DNA sequences from chloroplast (*rbc*L) and mitochondrial genes (*cox*I), Yang & Jin (2000) performed relative rate testing between *Metasequoia* and *Taxodium* using *Cunninghamia* R. Brown *in* A. Richard as an outgroup. For both the synonymous and non-synonymous sites, as well as the available plant fossil record, the *Metasequoia* lineage was calculated to have evolved at a slower rate than that of *Taxodium* following divergence from *Cunninghamia*. Thus, the available molecular evidence clearly indicates that rate heterogeneity between Sequoioideae and other lineages appears to be parallel across different genomes, implying that the same evolutionary process is responsible for the evolutionary slow down in the redwood clade, particular in *Metasequoia*. Using a chloroplast molecular clock, Li & Yang (2002) calculated a Jurassic (135.8 Ma) divergence time for the origin of the Sequoioideae. However, such a divergence time should be treated with caution as considerable rate heterogeneity for both synonymous and non-synonymous substitutions of the chloroplast genes have been detected in the Taxodiaceae (Yang & Jin, 2000). Such data undermine the direct application of the molecular clock approach to this plant group.

The available molecular data are in good agreement with the observed biochemical and morphological lines of evidence for evolutionary stasis for *Metasequoia* and other closely related redwood taxa. The conservative molecular evolution in *Metasequoia* is also reflected at the protein and metabolic levels. In leaves and stems of *Metasequoia*, Yang *et al.* (1999) detected the presence of atrial natriuretic peptides in a hormone that normally causes sodium and water excretion in animals. Hager & Wind (1997) constructed a *Metasequoia* endosperm cDNA library and characterized transcripts of legumin-encoding loci representing two divergent legumin gene subfamilies. Comparison of these amino acid sequences indicates that *Metasequoia* legumin precursors contain highly conserved sites for post-translational cleavage.

3.2. Population Genetics and Conservation

The morphology and anatomy of living *M. glyptostroboides* in its native population and *ex situ* cultivation have been extensively studied (Fulling, 1976; Kuser, this volume), but ecological data have been scarce after an early attempt to understand the habitat of its native population (Chu & Cooper, 1950). Using 46 single-tree seedlots germinated from seeds collected in 1990 from the Shui-sha-ba Valley, China, Kuser *et al.* (1997) conducted a frequency analysis using foliar allozymes to estimate the genetic diversity of its populations in both native and cultivated populations. While they detected that the single tree heritability remains higher than in other conifers, their allozyme data indicated an average to low genetic diversity that is accompanied by inbreeding and genetic differentiation for *ex situ* collections. Comparison of their data with those from the 40 cultivated trees derived from the initial seed dissemination in 1947, showed that the 1947 seedlots display an overall low genetic diversity but that the genetic stock of the cultivated trees in North America were unlikely to have been derived from a single tree.

To extend this study to the native population, we performed a RAPD analysis of 27 leaf samples collected from individual trees from the Shui-sha-ba Valley and its outlet sub-populations in Hunan and Sichuan Provinces in China (Li *et al.*, 1999). We were able to detect moderate genetic diversity with 53 percent polymorphic loci (PPL). This level of genetic variation is higher than that seen in *Cathaya argyrophylla* Chun & Kuang (32%), another endangered conifer in southern China, and *Picea mariana* (Miller) Britton, Sterns *et* Poggenburg (44%) from Canada using the same molecular technique. We found that the genetic distances among individual trees are primarily proportional to the geographic distances among different sub-populations. A recent AFLP analysis of 39 individual trees from the native *M. glyptostroboides* populations revealed the lack of spatial genetic flow and suggested that considerable genetic isolation of different sub-populations has occurred (Li *et al.*, 2003a). They further identified a 4–8 km range as being the effective barrier for *M. glyptostroboides* wind-pollination and believed that the tendency toward island distribution is the result of habitat fragmentation in the native *M. glyptostroboides* populations.

Recently, Leng *et al.* (2001) identified a rare Even Type cuticle from the inner surface of *M. glyptostroboides* leaves collected from an isolated *M. glyptostroboides* tree living in Paomu, Hunan Province, about 100 km away from the main Shui-sha-ba Valley population. After an intensive survey, it appears that such a unique cuticle type exists only in this particular tree. Yet, the common occurrence of this cuticle type in the fossil record (Leng, this volume) suggests that this micromorphological character is of an ancient origin. Recent genetic analysis using ITS sequences of nuclear ribosomal DNA confirmed the ancestral position of the Paomu tree (Li & Yang, 2003a). Using samples from different sub-populations, Li & Yang (2003a) sequenced 5.8S rDNA and its flanking ITS regions; phylogenetic reconstruction based on these DNA sequences places the Paomu tree at the most basal position with a strong bootstrap support. Thus, these data point toward the importance of the Paomu tree in both morphological variation and genetic diversity. Indeed, when the RAPD analysis included the Paomu tree, the population exhibits a moderate genetic diversity (53% PPL, Li *et al.*, 1999), whereas a recent study using the same technique, but excluding the Paomu tree resulted in a much lower value (38.6% PPL, Li *et al.*, 2003b). The genetic revelation confirmed Yang 's (1999) prediction that the isolated Paomu tree in Hunan Province not only preserves unique micromorphological characters, but enhances the overall genetic diversity of this relict population.

Molecular studies on the population genetic structure and diversity of *M. glyptostroboides* have a significant impact on strategies and decision making for both the *in situ* and *ex situ* conservation of this relict species. Despite the micromorphological variation found in the Paomu tree, the overall low genetic diversity for *M. glyptostroboides* poses a serious threat to the survival of its native population. Although *M. glyptostroboides* has been cultivated throughout the world, the restricted source of seeds has resulted in little genetic diversity among the cultivated trees and serious inbreeding depression has been observed (Kuser *et al.*, 1997). The molecular data suggest that plantations using genetic stock from several genetically distant sub-populations should be encouraged. These genetic studies also point out the need for protecting the native population, especially the isolated Paomu tree in the Hunan Province.

4. BIOCHEMISTRY OF ANCIENT BIOMOLECULES FROM FOSSIL *METASEQUOIA*

4.1. Polysaccharides and Bound Fatty Acids

Whereas studies of modern molecules revealed phylogenetic information and genetic structure for the living *M. glyptostroboides*, ancient biomolecules recovered from *Metasequoia* fossils can provide further evidence regarding molecular preservation, fossilization and paleoenvironmental conditions. Using the Py-GC-MS technique, Anderson & LePage (1995) reported on the preservation of diterpenoids and related products from resinites associated with fossil *Metasequoia* wood and cones from the Eocene Arctic site. Recently, we identified a set of pyrolysis products that indicate the presence of polysaccharides and fatty acids from these Tertiary Arctic *Metasequoia* leaf tissues (Yang *et al.*, in press). The pyrolysis markers (Figures 8-2 and 8-3) detected from *Metasequoia* fossil tissues indicate that polysaccharides from cellulose are preserved (Boon *et al.*, 1982; Pouwels *et al.*, 1989; Stankiewicz *et al.*, 1997; McCobb *et al.*, 2001). Cellulose is subject to rapid degradation during early diagenesis (Hedges *et al.*, 1985; Peulve *et al.*, 1996; Spiker & Hatcher 1987; van der Heijden & Boon, 1994). The occurrence of abundant polysaccharide moieties in the late Paleocene to early Eocene *Metasequoia*

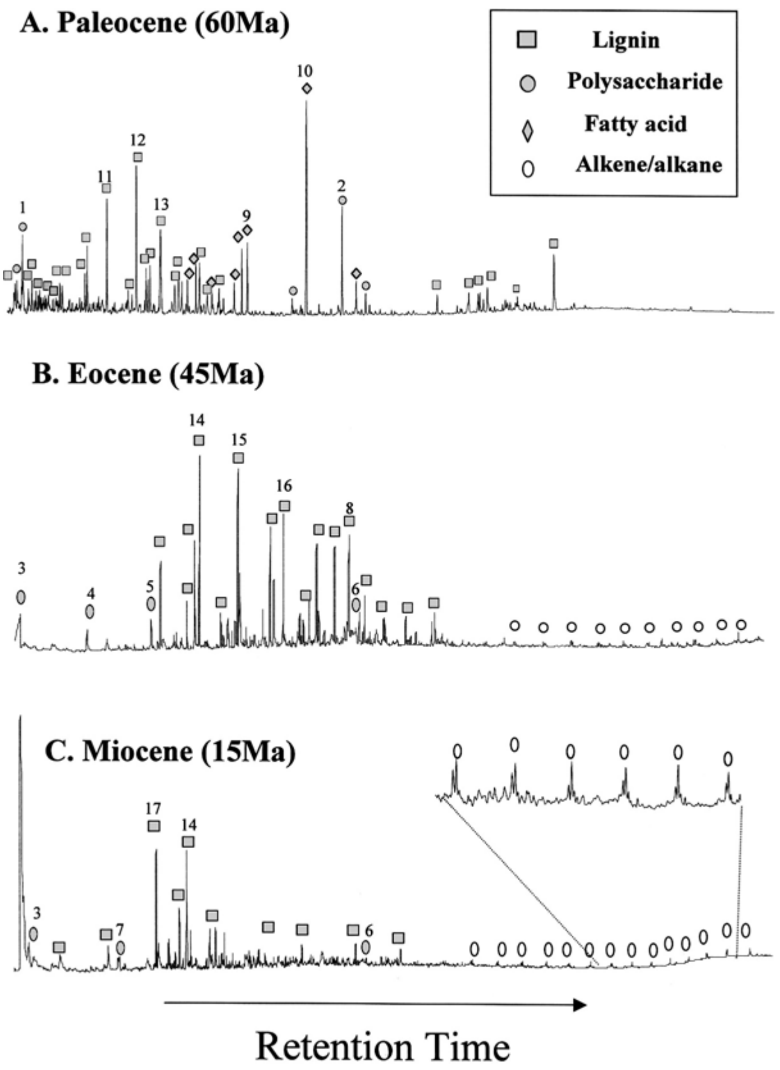
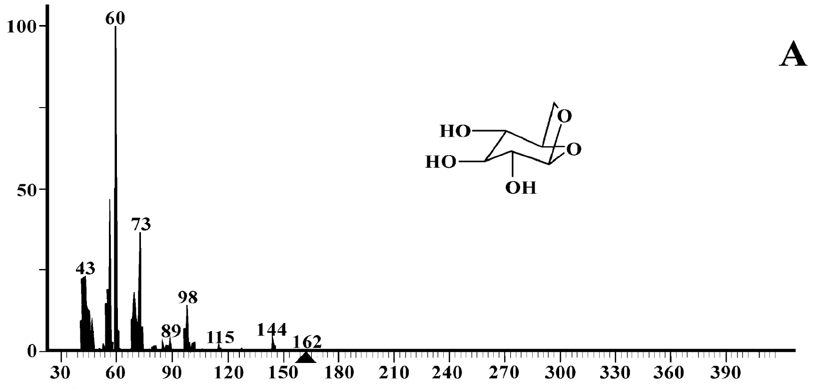
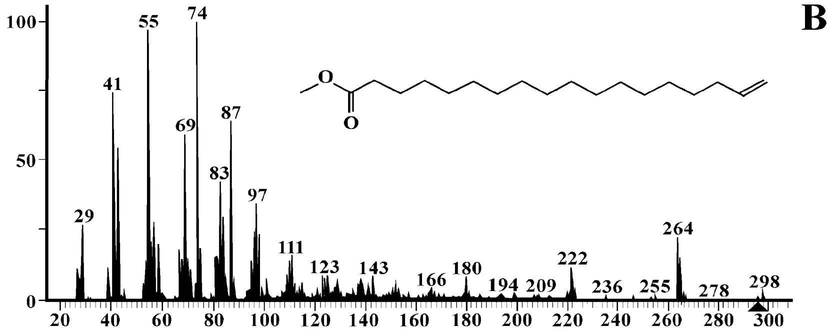


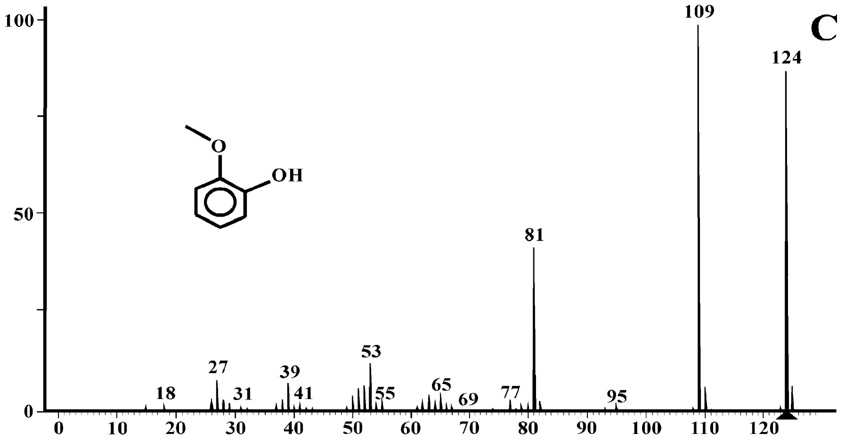
Figure 8-2. Representative ion chromatograms of Py-GC-MS pyrolysates showing the relative intensity of the pyrolysis products (vertical axis) obtained from *Metasequoia* leaf tissues of late Paleocene samples (treated with TMAH) (A), middle Eocene samples (without TMAH) (B), both from the Canadan Arctic, and middle Miocene Clarkia samples from northern Idaho (without TMAH), (C). Inserts in C illustrating the homologous series of *n*-alk-1-ene/*n*-alkane pairs. Identification of major peaks: 1. hydroxypropanone, 2. decenomic acid; 3. acetic acid; 4. 2-furaldehyde, 5. 5,6-dihydropyran-2,5-dione, 6. Levoglucosan, 7. 2-methyl-2-cyclopenten-1-one, 8. 4-acetyl-2-methoxyphenol, 9. meth-C$_{16:0}$ acid; 10. meth-C$_{18:0}$ acid, 11. 3,4-dimethoxy-benzaldehyde, 12. benzoic acid; 13. 4-methoxyphenyl-propenoic acid, 14. 2-methoxyphenol, 15. 2-methoxy-4-methylphenol, 16. 4-ethyl-2-methoxyphenol, 17. Phenol.



(R) 1,6-Anhydro-beta-D-glucopyranose (levoglucosan)



(M) 17-Octadecanoic acid, methyl ester



(R) Phenol, 2-methoxy-

Figure 8-3. Examples of MS spectra and chemical structures for inference of molecular preservation in fossil *Metasequoia* leaves (A) polysaccharides, (B) fatty acids, and (C) lignin (see Figure 8-2 for identification and detailed list is presented in Yang *et al.*, in press).

leaf remains from the Canadian Arctic perhaps represents the oldest molecules of these kinds that have been detected in the geological record using the online pyrolysis technique. These results are consistent with the isolation of purified cellulose from *Metasequoia* wood tissue recovered from the Eocene Napartulik locality on Axel Heiberg Island in the Canadian Arctic (Jahren & Sternberg, 2002, 2003; Jagels & Day, 2004).

By adding the chemical TMAH, a large amount of fatty acid moieties were detected from the late Paleocene to early Eocene Arctic fossil *Metasequoia* fossils (Figure 8-2A). The fatty acid moieties are dominated by C_{16} and C_{18} saturated (single bond) acids, which are associated with fewer amounts of unsaturated acids of the same carbon length. Prior to Py-GC-MS analysis, repeated solvent extraction performed on the sediment-free *Metasequoia* tissues should have removed free fatty acids associated with sediment matrix, leaf wax, and cell membrane. Although a bacterial origin of these fatty acids cannot be completely ruled out, the majority of detected fatty acids probably represent pyrolysis markers of cutin preserved in the *Metasequoia* leaf tissues (Tegelaar *et al.,* 1989; Stankiewicz *et al.*, 1998b). The minor components of unsaturated acids along with the presence of abundant methyl-phenols and limited polysaccharides are symptomatic of decayed leaf tissues found in higher plant (van Bergen *et al.*, 1997; Stankiewicz *et al.,* 1998b). As cutin acids are almost always degraded during early diagenesis (Gõni & Hedges, 1990; Eglinton & Logan, 1991; Opsahl & Benner, 1995), *in situ* fatty acids were rarely detected in plant fossils older than Quaternary age (review sees Briggs *et al.,* 2000 and references therein). Hence, the detection of *in situ* cutin acids in the late Paleocene to early Eocene *Metasequoia* leaf litters not only established an early record of cutin preservation, but they are also indicative of the high quality molecular preservation of these Arctic *Metasequoia* fossils. The extraordinary preservation of chloroplast and other leaf ultrastructures in these fossils (reviewed by Schoenhut, this volume) mirrors our observations. Despite the extraordinary preservation, however, an extensive search for ancient DNA from these *Metasequoia* tissues from the Arctic (E.M. Golenberg personal communication), Miocene Clarkia (Soltis *et al.*, 1992) deposits, and Eocene amber (Yang, 1999) have been unsuccessful.

4.2. Source and Role of Labile Biomolecules

The Arctic Tertiary *Metasequoia* remains were deposited in swamp or deltaic lowland environments (Ricketts & Stephenson, 1994; Kalkreuth *et al.*, 1996; McIver & Basinger, 1999), from which "Fossil *Lagerstätten*" (extraordinarily preserved fossil material) were occasionally reported (Allison & Briggs, 1991). However, the preservation of ancient labile biomolecules, such as polysaccharides and cutin acids, from fossils in such open terrestrial environments is rare. Scanning electron microscopy (SEM) observations indicate that the late Paleocene-early Eocene *Metasequoia* leaves are extremely well preserved anatomically, showing almost intact three-dimensionally preserved epidermal cells with distinct and continuous cuticular membrane (Q. Leng, unpublished data). If we assume that the fossil *Metasequoia* cell walls are composed of cellulose as is the case in *M. glyptostroboides*, then the observed thick and rigid amorphous materials in the cell wall of the Tertiary fossils should indicate cellulose polysaccharides, whereas the multi-layered cell membrane immediately below the surface wax layers should be a possible source of cutin acids. Furthermore, the combined pyrolysis data and SEM observations from these *Metasequoia* leaf fossils led us to believe that both polysaccharides and cutin acids were involved in mechanical support of three-dimensional preservation of fossils perhaps through physical networking and chemical bonding.

While the mechanical function of lignin in plant fossils is well documented (Taiz & Zeiger, 2002), it was not clear whether polymeric cellulose makes a significant contribution in the retention of the structural integrity of plant cellular tissues during fossilization. It has been shown that the cellulose content and integrity of the anatomical structures are closely linked in fossil plants (Barghoorn & Spackman, 1950; Hedges *et al.,* 1985; Hedges & Weliky, 1989; Benner *et al.,* 1990; Stout & Boon, 1994). It was further documented that in the absence of lignin, the strength of integration of structures can be maintained by a polysaccharide-tannin complex as revealed by molecular studies of the fruit walls of water lilies (van Bergen *et al.*, 1996). The detection of large amount of fatty acids in the Arctic *Metasequoia* samples, either physically trapped or chemically linked in the organic matrix, suggested that they may also play an important role in preserving the three dimensional anatomy of these Tertiary plant litters.

4.3. Lipids

The preservation of significant amount of lipids in both the Miocene Clarkia (up to 10 μg/g dry weight of n-alkenes, Lockheart *et al.,* 2000) and Eocene Arctic *Metasequoia* fossils (up to 5 μg/g dry weight of n-alkanes, H. Yang unpublished data) is not an unexpected result. These alkyl lipid classes are hydrophobic and therefore have a high preservational potential in the sedimentary record (Eglinton & Logan, 1991). However, the retention of taxon-specific lipid signatures over geologic time is rare, suggesting that evolutionary stasis of *Metasequoia* may also operate at the biochemical level. Lockheart *et al.* (2000) extracted lipid n-alkane and n-alkanol fractions from *Metasequoia* leaf tissues preserved in the Miocene Clarkia deposit and explored their chemotaxonomic values.

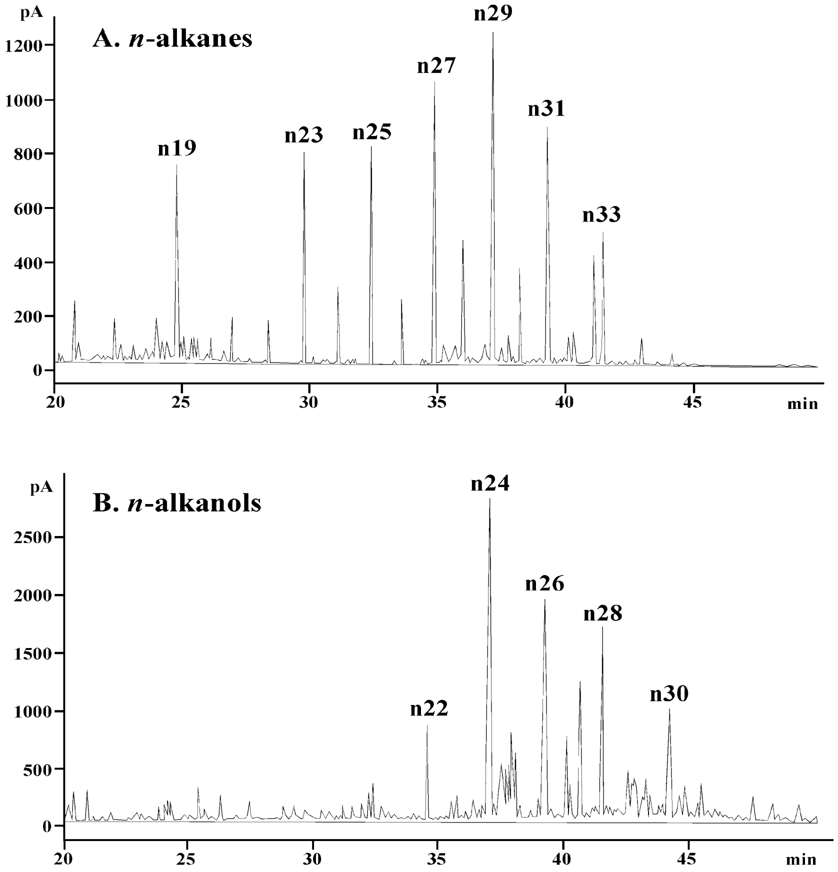


Figure 8-4. GC-FID spectra of *n*-alkanes (A) and *n*-alkanols (B) extracted from Tertiary *Metasequoia* leaves, Canadian Arctic.

In the *n*-alkane fraction, the *Metasequoia* fossils display a broad lipid distribution with C_{29} as the dominant peak followed by C_{31} and C_{35} carbon length, whereas in *n*-alkanols, the distribution is bimodal with C_{24} being the maximum peak followed by C_{28}. These profiles are found to be different from the sedimentary background and among different plant fossil taxa (Lockheart *et al.*, 2000; Briggs *et al.*, 2000). Recently, we obtained identical lipid distribution profiles for the two fractions of the Paleocene and Eocene Arctic *Metasequoia* litters (Figure 8-4). GC-FID spectra of both *n*-alkanes and *n*-alkanols representing leaf surface waxes extracted from these approximately 60 and 45 Ma year old *Metasequoia* leaves match the profiles obtained from the middle Miocene (15-16 Ma) *Metasequoia* from the Clarkia deposits (Lockheart *et al.*, 2000).

Given that the Arctic and Clarkia fossils clearly grew under different paleoclimatic conditions and were preserved in different depositional environments (Yang, 1996; Yang & Huang, 2003; LePage, personal communication), the similarity of *Metasequoia*-specific lipid profiles through geological time is consistent with the evolutionary stasis seen at the morphological level. In addition, a comparative study of modern *Metasequoia* lipids has shown that lipid profiles differ slightly between external wax and whole leaf lipid extractions (H. Yang, unpublished data). The hydrocarbon fraction (*n*-alkanes) extracted from surfaces of modern *Metasequoia* leaves are dominated by C_{25} peak, but the same fraction extracted from the whole leaf tissue produced a slightly different pattern with C_{29} as the dominating peak. Such variation may suggest a slightly different lipid pool in the internal leaf mesophyll in comparison with the external leaf wax as recently shown in the study of *Ginkgo* leaf tissues by Nguyen Tu *et al.* (2001). Because the whole leaf extraction procedure is always used for fossil lipid analysis, a better comparison with the ancient lipid from a known fossil taxon is to use both internal and external lipids (including both wax and mesophyll lipids) extracted from modern counterparts.

4.4. Bound Alkanes and Alkenes

Due to its chemical stability and widespread occurrence in petroleum, the chemically stable homologous series of *n*-alk-1-ene/*n*−alkane pairs are believed to play a major role in kerogen formation in ancient sedimentary rocks and are therefore important in hydrocarbon exploration. However, their origins have recently received extensive debates (Tegelaar *et al.*, 1989; de Leeuw *et al.,* 1991; Tegelaar *et al.*, 1991; Collinson *et al.,* 1998; Briggs, 1999; Stankiewicz *et al.*, 1998b, 2000). Traditionally, the occurrence of homologous series in ancient sediments was explained by one of the two following models: random repolymerization (Tissot & Welte, 1984) or selective preservation (Nip *et al.,* 1986; Tegelaar *et al.*, 1989; de Leeuw *et al.*, 1991). Recently, an alternative hypothesis proposed that these homologous pairs might have originated from *in situ* polymerization during early diagenesis of leaf tissues (Collinson *et al.*, 1998, Briggs *et al.*, 1998; Briggs, 1999; Stankiewicz *et al.,* 1998b, 2000).

Although a precise mechanism is still elusive, our data based upon the comparison of pyrolysis products from *Metasequoia* tissues at various stages of alteration seem to support *in situ* polymerization during early diagenesis of leaf material. The homologous series of *n*-alk-1-ene/*n*-alkane pairs were not detected in leaf tissues of modern and the better-preserved late Paleocene-early Eocene *Metasequoia* samples, indicating that these components probably are not present as original components in *Metasequoia*. This has also been reported in other plant taxa (Mösle *et al.,* 1997; Collinson, 1998; Stankiewicz *et al.,* 1998a). Given the evolutionarily conservative nature of *M. glyptostroboides*

(Chaney, 1951; Liu *et al.*, 1999; Yang & Jin, 2000), it is reasonable to believe that ancient *Metasequoia* did not contain these “cutan” markers as an original molecular inventory. The fact that these compounds were only found in leaf tissues that have undergone further alteration (such as in the middle Miocene Clarkia material, Figure 8-2C) provides evidence for the formation of the aliphatic markers within the *Metasequoia* leaf tissues during diagenesis (i.e., through *in situ* polymerization). Thus, a logical explanation for our data is that the presence of these homologous pairs in the Miocene *Metasequoia* samples reflected leaf tissue alteration as a consequence of diagenetic effects. Furthermore, since our tested early Tertiary *Metasequoia* tissues were obtained free of sedimentary matrix, the origin of these components has to be endogenous, rather than contamination/migration from random polymerization of exogenous biomolecules in the sediments (Yang *et al.*, in press).

5. FOSSIL TAPHONOMY AND PALEOENVIRONMENTAL APPLICATIONS

5.1. Molecular Taphonomy

The combination of molecular-level characterization and SEM observations may detect subtle preservational differences that otherwise may not be recognizable at the gross morphological level. Based on Py-GC-MS data, the molecular preservation in some Tertiary *Metasequoia* leaf samples can be ranked, and this rank order is supported by SEM observation at the micromorphological level (Yang *et al.*, in press). It is clear that the quality of molecular preservation in fossil *Metasequoia* tissues is not controlled by the age of these materials alone, confirming a phenomenon that has been proposed previously in studies of other well preserved fossils (Stankiewicz *et al.*, 1997; Briggs *et al.*, 2000).

In general, tissues in taxodiaceous species are not known to have high degradation rates (Webster & Benfield, 1986). Yet, the massive amount of leaf litter produced by the Arctic *Metasequoia* during the Tertiary represents a significant carbon accumulation rate in the polar region (Schlesinger & Lichter, 2001; Royer *et al.,* 2003). A better understanding of the molecular mechanism, especially oxidation, hydrolysis, and microbial degradation that are known to control the rate of litter decomposition, may hold a key to better elucidating the mode of fossilization for these materials and hence the impact on carbon cycles during the early Tertiary in polar regions (Eglinton & Logan, 1991; Lindhal, 1993; Briggs *et al.*, 2000). As both the Arctic and the Clarkia deposits accumulated rapidly under shallow and anoxic conditions (Smiley & Rember, 1981, 1985; Yang, 1993; Ricketts & Stephenson, 1994; Kalkreuth *et al.*, 1996), the reducing environments at these sites must have facilitated the preservation of labile biomolecules. As hydrolytic attacks are known to break down labile biomolecules such as DNA and carbohydrates, hydrolysis has been attributed as a main degradation agent for the Arctic *Metasequoia* fossils (Blanchette *et al.*, 1991; Obst *et al.,* 1991). However, both leaf and wood tissues found in the Arctic sites were waterlogged (Basinger, 1991; Francis, 1991; Grattan, 1991; Williams *et al.*, 2003b) and the water-saturated conditions for the Clarkia fossils are well known (Pääbo & Wilson, 1991; Yang & Huang, 2003). Thus, the high quality of molecular preservation seen in these samples is inconsistent with the notion that hydrolysis alone is capable at degrading biomolecules in plant tissues, especially considering the large quantity of polysaccharide preservation found in the Arctic specimens. Finally, anaerobic bacterial degradation is known to selectively remove polysaccharides (Benner *et al.*, 1984) and sterile conditions were unlikely in such open environments for the Arctic sites. In addition, the current low temperature at the Arctic area is unlikely responsible for the extraordinary preservation, as recent molecular studies have revealed an extensive cellulose-degrading microbial activity under snow (Schadt *et al.*, 2003). It is presently not clear to what extent and in what manner those microorganisms were involved in the degradation of the Arctic *Metasequoia* fossils. If bacteria or other microbes were present, but did not cause significant decay to these fossil materials, especially given the large quantity of carbohydrates, then an unknown mechanism must have been in place to inhibit microbial attacks on these *Metasequoia* tissues.

5.2. Paleophysiological and Paleoclimatic Signals

Metasequoia glyptostroboides is one of a few conifers that exhibit a deciduous habit. Its distribution and dominance in deciduous floras throughout the Tertiary polar regions where the duration of winter darkness exceeded three to four months per year makes this species an attractive candidate for investigations of physiological adaptation of the deciduous habit (Wolfe, 1987; Royer *et al.*, 2003; Jagels and Equiza, this volume; Vann, this volume). Molecular phylogeny based upon DNA sequences clearly indicates that modern taxodiaceous species with deciduous habits (i.e., *Metasequoia*, *Taxodium*, and *Glyptostrobus*) are placed in separate branches on the phylogenetic tree (tsumura *et al.,* 1995; Gadek *et al.*, 2000; Kusumi *et al.,* 2000; Li & Yang, 2003b). *Metasequoia* is more closely related to evergreen species *Sequoia* and *Sequoiadendron* than the deciduous *Taxodium* and *Glyptostrobus*. In addition, the subfamily Sequoioideae (consisting of *Metasequoia*, *Sequoia* and *Sequoiadendron*) originated earlier than some of the other genera of the Taxodioideae (consisting of closely allied deciduous taxa *Taxodium* and

Glyptostrobus) and the evergreen taxon *Cryptomeria*. Thus, the separate origins of deciduous taxa within the Taxodiaceae-Cupressaceae complex suggests that the deciduous character evolved at least twice within this group, once in *Metasequoia* and the second time in the unknown common ancestor leading to *Taxodium* and *Glyptostrobus* (Kusumi *et al.*, 2000).

Because of its widespread fossil distribution, distinguished morphological characters, and restricted climatic range for its living population, fossil *Metasequoia* has been used by paleobotanists to indicate paleoclimatic conditions using the nearest living relative approach (e.g., Boyd, 1990; Greenwood & Wing, 1995). However, the accuracy of such an approach, especially dealing with the cold month minimum temperature, has recently been challenged based on observations of *Metasequoia* and other "living fossils" (e.g., *Ginkgo* L.) that display an increased freezing sensitivity under high CO_2 concentration (Royer *et al.*, 2002). Recently, Jahren & Sternberg (2002, 2003) and Jagels & Day (2004) have measured bulk C isotope values from purified cellulose isolated from the Canadian Arctic *Metasequoia* fossils and suggested that the Eocene pCO_2 was no higher than the present day level (Jagels & Day, 2004), a conclusion that supports one of the recent paleobotanical investigations (Royer *et al.*, 2001). Analyses of both oxygen and hydrogen isotope signals from fossil cellulose from *Metasequoia* indicate a humid climatic condition caused by meridional weather patterns at the Eocene Arctic (Jahren & Sternberg, 2002, 2003). While *Metasequoia* gained the ability to adapt to high pCO_2 over geological time remains largely unknown, it is anticipated that further molecular level isotope analyses of modern and fossil *Metasequoia* hold potentials to elucidate additional paleophysiological and paleoclimatic data.

6. GENERAL IMPLICATIONS AND CONCLUSIONS

Molecular level investigations on living and fossil *Metasequoia* have broadened our view of the evolutionary history of this genus and also shed light on its fossilization, preservation, and physiological adaptations to unique physical conditions in the geologic past. Such information has added to our general understanding of the molecular mechanisms governing evolution, phylogeny, and taphonomy. In conjunction with morphological observations and physiological experimentation, molecular studies on *Metasequoia* has enhanced our ability to conserve and manage this relict species in its native Chinese populations. In summary, molecular studies of *Metasequoia* have contributed to the following specific aspects in our understanding of its biological and geological history:

(1) Phylogenetic analyses based on protein and nucleotide sequences from modern samples have placed *Metasequoia* as the sister taxon with *Sequoia*

and *Sequoiadendron*. These genera form the subfamily Sequoioideae and occur as one of the basal groups within the Taxodiaceae-Cupressaceae complex, confirming the systematic treatment by morphologists. Relative rate testing based on multi-gene DNA sequences provides a quantitative assessment of the "slowdown" in the substitution rate in the Sequoioideae lineage, providing a molecular correlation with observed evolutionary stasis at the morphological and biochemical levels.

(2) Molecular evidence has revealed a low population genetic diversity in native *M. glyptostroboides* populations and a lack of spatial genetic structure resulting from habitat fragmentation in its native habitat in southern China. An isolated tree in Paomu, Hunan Province was found to carry ancestral micromorphological characteristics, which subsequently increased the genetic variability of the entire living population. This information allows important guidelines and critical decisions to be made regarding the management and conservation of its native populations in China.

(3) Molecular and biochemical investigations into well-preserved Tertiary fossil *Metasequoia* remains show the preservation of labile biomolecules such as carbohydrates. Comparative geochemical and SEM analyses revealed the source of these chemically unstable biomolecules and suggested that they carry important structural functions to support the integrity of fossil morphology. Comparative studies of biomolecules from Tertiary fossil *Metasequoia* shed light on the origin of homologous series of *n*-alk-1-ene/*n*-alkane pairs preserved in the geological record.

(4) Molecular taphonomic studies on well-preserved *Metasequoia* fossil tissues support the idea that anoxia is critical to the long-term preservation of labile biomolecules in *Metasequoia*, but the role of hydrolysis in molecular degradation needs to be further evaluated. Current data suggest that a mechanism that prevents complete microbial degradation of these well-preserved *Metasequoia* tissues is likely responsible for the preservation of *in situ* labile biomolecules in the early Tertiary *Metasequoia* found in the Canadian Arctic. The high quality molecular preservation in the Arctic *Metasequoia* tissues warrants further molecular level investigations targeting various biological and geological questions.

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9. APPENDIX A

Metasequoia glyptostroboides nucleotide sequences available from GenBank.

Locus	Coding protien	Genome	Length (bp)	GenBank#	References
*rps*4	Small ribosomal protein 4	cpDNA	410	AY188268	Cranfill, R. & D. Kelch, unpublished
ITS	*Pet*G-*trn*P intergenic spacer region	cpDNA	245	AY291319	Li, T.-Y. & X.-Y. Chen, unpublished
*atp*1	ATPase alpha subunit	mtDNA	1205	AF197619	Qiu *et al.*, 1999
*atp*B	ATPase beta subunit	mtDNA	1129	AJ235534	Savolainen *et al.*, 2000
*m*RNA	fructose-1, 6-diphosphate aldolase	cpDNA	1504	AF521254	Zhang, X.-N. *et al.*, unpublished
*m*RNA	fructose-1, 6-diphosphate aldolase	cpDNA	1200	AF521253	Zhang, X.-N. *et al.*, unpublished
*chi*1	Chitinase class I	rDNA	273	AB077019	Kusumi *et al.*, 2002
RabMet-B	Rab geranylgeranyl transferase beta subunit	rDNA	1141	AB076999	Kusumi *et al.*, 2002
RabMet-A	Rab geranylgeranyl transferase beta subunit	rDNA	1142	AB076998	Kusumi *et al.*, 2002
*gap*C	glyceraldehyde-3-phosphate dehydrogenase	rDNA	2108	AB076713	Kusumi *et al.*, 2002
Myb	Myb transcription factor	rDNA	913	AB076593	Kusumi *et al.*, 2002
*chi*2	Chitinase class III	rDNA	646	AB075591	Kusumi *et al.*, 2002
*hem*A	Glutamyl-tRNA reductase	rDNA	1047	AB075575	Kusumi *et al.*, 2002
ferr	Ferredoxin	rDNA	346	AB075539	Kusumi *et al.*, 2002
*chi*1	Chitinase class I	rDNA	339	AB075370	Kusumi et al., 2002
26S rRNA	26S ribosomal RNA	rDNA	1054	AY056512	Rydin, C. *et al.*, unpublished
CAD	Cinnamyl alcohol dehydrogenase	mtDNA	1363	AF146013	Wang, X.Q., unpublished
*phy*N1	Phytochrome N1	cpDNA	576	AJ420753	Schmidt, M. *et al.*, unpublished
*phy*O	Phytochrome O	cpDNA	543	AJ420754	Schmidt, M. *et al.*, unpublished
*mat*K	Maturase	cpDNA	1595	AB030122	Kusumi *et al.*, 2000
*Chl*L	Chloroplast large unit of light-independent protochlorophyllide reductase	cpDNA	738	AB030096	Kusumi *et al.*, 2000
*trn*L	tRNA-Leu	cpDNA	528	AB030050	Kusumi *et al.*, 2000
*trn*F	tRNA-Phe	cpDNA	329	AB029854	Kusumi *et al.*, 2000
*ndh*F	NADH dehydrogenase	cpDNA	375	U30902	Neyland & Urbatsch, 1996
ITS rRNA	18S internal transcribed spacer 1, 5.8S ribosomal RNA from CQO1	rDNA	1092	AF387530	Li & Yang, 2003a

(*Continued*)

Locus	Coding protien	Genome	Length (bp)	GenBank#	References
ITS rRNA	18S internal transcribed spacer 1, 5.8S ribosomal RNA from SZ01	rDNA	1092	AF387529	Li & Yang, 2003a
ITS rRNA	18S internal transcribed spacer 1, 5.8S ribosomal RNA from NJ01	rDNA	1092	AF387528	Li & Yang, 2003a
ITS rRNA	18S internal transcribed spacer 1, 5.8S ribosomal RNA from PM01	rDNA	1092	AF387527	Li & Yang, 2003a
ITS rRNA	18S internal transcribed spacer 1, 5.8S ribosomal RNA from MD01	rDNA	1094	AF387526	Li & Yang, 2003a
28S rRNA	28 Small ribosomal subunit RNA	rDNA	601	AY034044	Li & Yang, 2003a
*mat*K	Maturase	cpDNA	1530	AF152203	Gadek *et al.*, 2000
*frx*C	Chloroplast product	cpDNA	708	AF380275	Li, C. & Q. Yang, unpublished
*rbc*L	Large subunit of ribulose-1, 5-bisphophate carboxylase/oxygenase	cpDNA	1428	AJ235805	Chase, 1993
ChlB	Chloroplast subunit of light-independent protochlorophyllide reductase	cpDNA	38	X98574	Karpinska et al., 1997
*atp*A	F1 ATPase alpha subunit	mtDNA	1031	AF209107	Bowe *et al.*, 2000
*cox*I	Cytochrome C oxidase	mtDNA	1406	AF020569	Bowe *et al.*, 2000
*Chl*B	Chloroplast subunit of light-independent protochlorophyllide reductase	cpDNA	309	L25769	Boivin *et al.*, 1996
18S rRNA	18 Small ribosomal subunit RNA	rDNA	1714	L00970	Savard *et al.*, 1994
MgLeg4	Legumin	rDNA	1652	X95544	Hager & Wind, 1997
MgLeg26	Legumin	rDNA	1624	X95546	Hager & Wind, 1997
MgLeg18	Legumin	rDNA	1667	X95545	Hager & Wind, 1997
Phymeta1	Phytochrome	cpDNA	569	X80297	Kolukisaohlu, H.U. *et al.*, unpublished
5S rRNA	5 Small ribosomal subunit RNA	rDNA	120	M10432	Hori *et al.*, 1985

PART III

Ecology and Ecophysiology

Chapter 9

Ecological Characteristics of *Metasequoia glyptostroboides*

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Abstract: *Metasequoia* Miki is a deciduous conifer with a highly restricted natural distribution in central China. It is a riparian species that thrives under conditions of abundant growing season moisture availability, although as is shown by its distribution in cultivation, it is capable of sustained growth under drier conditions as well. Whereas the variability of climate across its natural range is minute, under cultivation it grows across a gradient of 16.3°C of mean annual temperature and 2360 mm of mean annual precipitation. No cultivated *Metasequoia glyptostroboides* Hu *et* Cheng are known to exist without supplemental water in areas that receive less than ca. 500 mm of mean annual precipitation. *Metasequoia glyptostroboides* grows tall quickly and is capable of obtaining stem lengths in excess of 30 m in less than 50 years. Based on measurements of the trees from its natural range, maximum height may be just over 50 m. Analysis of growth performance of *M. glyptostroboides* through time indicates that trees from different seedlots grown in common garden experiments remain static in their relative growth

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rates through time; trees that grew quickly from the outset continued to outpace slower growing trees eight years later. A mixture of environmental factors may alter *M. glyptostroboides* growth form. Most notably, shrubby varieties are known from a mixture of cold climates, but are not always found in extremely cold areas.

Key words: cultivar, climate, dawn redwood, geographic range, growth rate.

1. INTRODUCTION

Metasequoia glyptostroboides Hu *et* Cheng, also called dawn redwood, or water-fir (Shui-sha-ba) is a rare deciduous taxodioid conifer of the family Cupressaceae. It is the single species in the genus. Its present natural range is limited to small, highly disturbed areas of western Hubei, northern Hunan and eastern Sichuan provinces in central China (Chu & Cooper, 1950; Fu & Jin, 1992). *Metasequoia* Miki was known initially from fossil material (e.g., Miki, 1941) and was widely distributed across many different habitats as early as the Late Cretaceous period (Yang & Jin, 2000; LePage *et al.,* this volume; Meyer, this volume; Momohara, this volume). It was not until 1948 that extant *M. glyptostroboides* was described in the scientific literature as a new species (Hu & Cheng, 1948) and thus, earned the title of "living fossil".

Soon after the formal description of *M. glyptostroboides* as a new species, ecological studies were conducted on the main population of *M. glyptostroboides* (Chu & Cooper, 1950; Gressitt, 1953). This early research brought several issues to light: (1) The natural habitat of *M. glyptostroboides* was heavily impacted by human activity; (2) the distribution of many of the trees in the valley may be the result of transplantation by humans; and (3) remaining stands of *M. glyptostroboides* were highly fragmented and likely to bear the legacy of human land use and land change. Seed was collected from several populations in China and these were distributed worldwide in an effort to prevent extinction of the species (see Merrill, 1948; Kuser, 1999; Ma, 2003). This effort proved successful. Seedlings from the initial seed lot were planted throughout the world and today, trees are growing in botanical gardens and arboreta on every continent except Antarctica (see Satoh, 1999). In fact, this unintended experiment has revealed a wide range in tree morphology and a striking dichotomy between the environmental conditions of its current natural range and the environmental conditions the tree is capable of tolerating when cultivated.

The growth of *M. glyptostroboides* has been well studied from many different perspectives (e.g., ecological, genetic, horticultural, etc.). In light of the highly disturbed nature of native *M. glyptostroboides* stands, these data become extremely important in understanding the growth and ecology of a plant that has been known to western science for little more than half a century. Knowledge of its physical and environmental tolerance are important for understanding how *M. glyptostroboides* became so highly restricted in its natural distribution and for understanding how the native populations may respond to different conservation efforts. Furthermore, this information is useful to those engaged in studies of the biogeography and paleoecology of *M. glyptostroboides*. This paper reviews and updates information concerning the ecological characteristics of *M. glyptostroboides* growing under natural and cultivated conditions.

2. HABITAT AND NATIVE RANGE

Metasequoia glyptostroboides is a riparian species that is restricted to wet lower slopes and montane river and steam valleys in its native range (Chu & Cooper, 1950). The Shui-sha-ba Valley (30°10'N, 108°35'E) is located in a karst landscape characterized by both irregular topography and interrupted drainage networks (Figure 9-1). The dominant lithology of the area is Jurassic

Figure 9-1. Karst topography of the Shui-sha-ba Valley, Hubei Province China. The view is towards the south along the western wall of the valley. Note automobiles for scale. Photo by B.A. LePage.

sandstone that overlies Permian limestone. Most of the native population of *M. glyptostroboides* is found in an enclosed or blind valley at an elevation of 1050 m. The valley floor is relatively flat, predominantly underlain by Jurassic sandstone and has a drainage system dominated by the Modao River. This river terminates at the base of a Permian limestone cliff and re-emerges at the surface 10–20 km to the southeast. Soil parent material is predominantly sandstone, although in the lowland areas there is a mixture of limestone and sandstone derived sediments. The oldest trees are growing on acidic yellow-earth soils (Fu & Jin, 1992). Several of the stands on steep slopes appear to be growing on old deposits of colluvial material, possibly old landslide or debris flow deposits (Williams, personal observation).

It is difficult to define the extent of the pre-settlement distribution of *M. glyptostroboides* in China although it was likely greater than the present distribution (Ling, 1976; Litoff, this volume). Several populations of *M. glyptostroboides* exist as isolated stands within an approximately 800 to 1000 km^2 region of Hubei, Sichuan and Hunan Provinces. It occurs as a constituent of the Mixed Mesophytic Forest and grows at elevations ranging from 800 to 1500 m (Fu & Jin, 1992). In extreme cases, unique, single-tree outliers exist away from the main populations (see Leng, this volume). Chu & Cooper (1950) reported that the largest population was centered in a 25 km long and 1.5 km wide area along the Modao River in the Shui-sha-ba Valley, Lichuan County, Hubei Province. Small stands (often less than 30 individuals) are scattered throughout this strip of land. Wang & Guo (2002; cited in Ma, 2003) state that the *M. glyptostroboides* population in Lichuan County comprised 5746 trees (diameter > 20 cm measured at 1.3 m above the ground) in 1986–1988. There are also scattered individuals in the Lonshan area of Hunan Province (ca. 100 km south east of the Shui-sha-ba Valley) and in Shizhu, Sichuan province (ca. 75 km south west of the Shui-sha-ba Valley).

Several lines of evidence suggest that *M. glyptostroboides* may have been more widely distribution in the recent past. These include: (1) the aforementioned single tree outliers that may pre-date extensive human settlement of the region about 200 to 300 years ago and (2) sub-fossil remains of *Metasequoia* wood found in peat deposits in the Shui-sha-ba Valley and as far away as Wuhan, China (Bartholomew *et al.*, 1983; Kuser, 1999; Yang *et al.*, 2004). Finally, there is historical evidence (see Litoff, this volume) that *M. glyptostroboides* may have existed in other areas of China as late as the 1920s. There is a general consensus that human activity and expansion of agricultural activities played some role in the recent range contraction of *M. glyptostroboides*. This idea is supported by palynology studies that have correlated decreases in the amount of forested land cover with the expansion of agriculture in neighboring regions of China (Jiang & Piperno, 1999; Ren, 2000; Yi *et al.*, 2003).

2.1. Climate of Native Range

The climate of the Shui-sha-ba Valley is characterized as a temperate mesothermal climate with a winter dry season (Köppen class Cwa). Chu & Cooper (1950) noted that climate data for the Shui-sha-ba Valley are "extremely scanty" and the situation has not improved much since their initial assessment. Nevertheless, climatic conditions of the native range of *M. glyptostroboides* are of great interest to botanists and paleobotanists interested in understanding the environmental tolerances of *Metasequoia* in the present and in the geologic past. A lack of recording stations located in the Shui-sha-ba Valley led Chaney (1948) to use climate data collected in Chungking (ca. 200 km to the SSW) to estimate climate in the Shui-sha-ba Valley. When compared with local data the Chungking data are not a good proxy for the climate conditions in the valley. Bartholomew *et al.* (1983) present data from a weather station in Lichuan about 40 km northeast of the Shui-sha-ba Valley that is more reflective of the climate conditions that the *M. glyptostroboides* populations experience. These data are illustrated in Figure 9-2 as a Walter-Lieth climate diagram (*sensu* Walter & Lieth, 1969). Mean annual temperature (MAT) is ca. 13°C and the minimum monthly mean temperature is –6.1°C (absolute minimum temperature –15.4°C), the monthly mean maximum temperature is 32.3°C (absolute maximum 35.4°C) (Bartholomew *et al.*, 1983). Rainfall is seasonal with a mean annual precipitation of 1283 mm (climate data from Lichuan [1959–1978] as presented by Bartholomew *et al.,* 1983).

There are also fragmentary climate data from the Lichuan County Climate Report for the village of Xiaohe located inside the Shui-sha-ba Valley (Hong Yang, personal communication, 2004). Interestingly, the Xiaohe data (MAT = 12.7, MAP = 1260 mm) portray a nearly identical climate to that of Lichuan City. Clearly, a longer local climate record would better define the actual climate regime within the native range of *M. glyptostroboides* and enhance our understanding of the environmental factors that may limit the distribution of *M. glyptostroboides*.

It is interesting to note that the drier months coincide with the leafless period of this seasonally deciduous plants growth cycle. Whether seasonal aridity or some other factor triggers leaf fall in this plant is not known (see Vann, this volume). It is evident from the climate data that there is abundant growing season moisture availability. A water balance index is built into Walter-Lieth climate diagrams where one degree of temperature (Celsius) is equal to two millimeters of precipitation in the scaling of the two axes. This is based on the assumption that monthly potential evapotranspiration (in millimeters) is roughly equal to twice the mean monthly temperature (Gaussen, 1954). Wherever the precipitation curve drops below the temperature curve, a drought

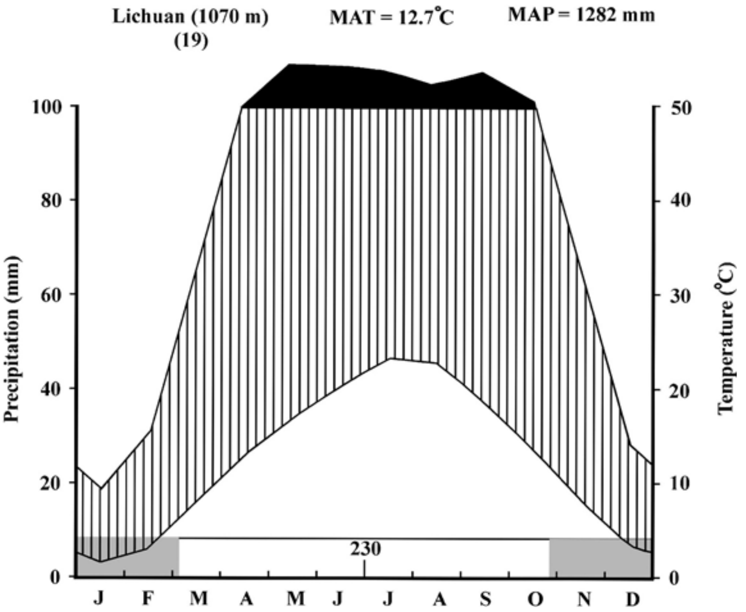

Figure 9-2. Climate diagram (sensu Walter & Lieth 1969) for Lichuan City, approximately 40 km from the main *M. glyptostroboides* population in the Shui-sha-ba Valley, Hubei Province, China. The shaded area along x-axis indicates times when frost is possible. Mean maximum and minimum and extreme maximum and minimum temperatures appear at the top and bottom of the temperature axis. Solid area of the precipitation curve indicates months in which mean monthly precipitation is in excess of 100 mm. Vertical lined area between precipitation and temperature curves indicates time of abundant moisture. Climate data are those reported by Bartholomew *et al.*, 1983 for the record period 1959–1978.

season is indicated. On the diagram of the Lichuan City data the precipitation curve is always above the temperature curve indicating a relative abundance of moisture throughout the year.

It could be argued that the Walter-Lieth approximation to water availability is overly simplistic because temperature and evaporation do not scale linearly. I also calculated an estimate of annual potential evapotranspiration (PET) throughout the year using the method of Thornthwaite (1948) and Thornthwaite & Mather (1957). This approach calculates the PET as a nonlinear function of temperature. Using these more robust estimates of PET paired with precipitation data for Lichuan, I generated a moisture index based on the balance between monthly precipitation and estimated PET. This approach, like the Walter-Lieth approach, reveals that precipitation exceeds PET even during the winter dry season. The mean annual water surplus for Lichuan is approximately 644 mm. The lack of a seasonal water deficit is particularly interesting when one considers where *M. glyptostroboides* has been artificially established.

In nearly all cases ample growing season water availability appears to be pivotal to it success (see below).

2.2. Geographic Distribution of Cultivated *Metasequoia*

Following its discovery as a living species there was an intense effort to cultivate *M. glyptostroboides* in many different environments. Today, there are solitary and multiple trees planted in groves growing in numerous locations throughout the world. The most northerly *M. glyptostroboides* I am aware of in North America are growing in Sitka, Alaska. In Europe, *M. glyptostroboides* are growing in cities as far north as Oslo, Norway and Helsinki, Finland. The southernmost *M. glyptostroboides* in North America are growing in New Orleans, Louisiana. In short, it has a large geographic distribution under cultivation. It is surprising that a species that has such a restricted natural distribution would do so well as a cultivated species. *Metasequoia glyptostroboides* has become a favored horticultural tree in Europe, North America and Asia (see Kuser, this volume). For example, Hendricks & Søndergaard (1998) estimate that in Denmark alone there may be in excess of 50,000 trees in cultivation. As noted by others (e.g., Kuser, 1999) *M. glyptostroboides* grows robustly throughout much of eastern North America. Although no such estimate for North America has been made it likely enjoys a high planting rate and large population sizes similar to those found in Europe.

The spread of *M. glyptostroboides* as a horticultural and forest product species provides some additional data on this species climatic tolerance. Figure 9-3 is a plot of the climate space that *M. glyptostroboides* currently occupies as a cultivated species. It is apparent that *M. glyptostroboides* is capable of growing over a wide range of mean annual temperature (min. = 4.5°C, max. = 20.8°C) and precipitation (min. = 497 mm, max. = 2859 mm). It is note worthy that there appears to be a lower threshold of about 500 mm of mean annual precipitation below which the species does not thrive without supplemental water. This corroborates the observations of others who note that the performance of *M. glyptostroboides* appears to be tightly coupled with water availability (Pokorný, 1981; Buffi, 1987; Kuser, 1999; Xie *et al.,* 1999; Williams *et al.,* 2003). In these areas, seasonal water deficit may prevent long-term survival of *M. glyptostroboides*. This may explain the noticeable lack of *M. glyptostroboides* being cultivated in Mediterranean climates.

However, this species does seem to tolerate slightly drier and more continental climates like that of Europe. Because *M. glyptostroboides* is a seasonally deciduous tree the seasonal pattern of precipitation may be more important than the absolute amount of precipitation for the species to survive. Ample growing season water availability is a prerequisite for plant growth. For example,

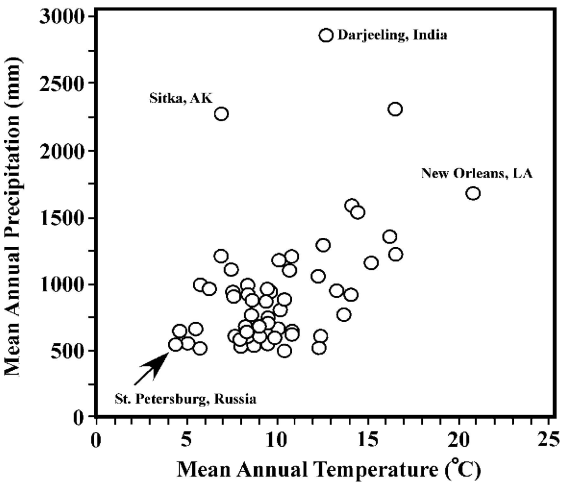

Figure 9-3. Climate conditions across the cultivated range of *M. glyptostroboides*. Each point on the scatter plot represents a location where *M. glyptostroboides* is currently growing. Location data are from published reports by Satoh (1999), Kuser (1983), Goudzwaard & Schmidt (1992) and Williams (unpublished data). Climate data are from NOAA NCEP Global Monthly Data Set.

the climate of Copenhagen is cool and fairly dry (MAT = 7.8°C, MAP = 590 mm), yet *M. glyptostroboides* grows quite well attaining tree heights of 25 m in 50 years (Hendricks & Søndergaard, 1998). At the Kórnik Arboretum in Kórnik, Poland, 25-year-old *M. glyptostroboides* growing on moist peat soil performed better than trees growing on a dry sandy soil with a deep water table (below 2 m; Bugala, 1984). *Metasequoia glyptostroboides* introduced to southern Switzerland in trial plantings experienced high mortality and poor tree growth (tree height averaged only 3.5 m after 18 years) apparently due to insufficient growing season precipitation (Buffi, 1987; P. Rotach, personal communication, 1999).

Interestingly, *M. glyptostroboides* is relatively cold tolerant and persists in colder locations such as St. Petersburg, Russia and the northeastern United States. The tree buds are able to survive cold temperatures down to −30°C Sakai (1971). This seems to match the cold climate limits on the distribution of *M. glyptostroboides*. There are accounts of the plant suffering terminal leader loss and decreased vigor due to late spring freezing events (Pokorný, 1981; Bulygin, 1989).

Although *M. glyptostroboides* has not yet established wild populations in areas surrounding planted trees, it may be only a matter of time. The plant is now reproducing naturally and seedlings have established in several areas. Kuser (1984) reports seedlings emerging on areas of a suburban lawn scraped clean of grass by a snowplow in Princeton, New Jersey. I have observed young saplings (less than 4 yr old) growing on mineral soil near a 42 year-old plantation of *M. glyptostroboides* in Kyoto, Japan (Williams, personal observation). In some cases, solitary trees are producing viable offspring. On the campus of Franklin and Marshall College, in Lancaster, Pennsylvania, numerous seedlings germinate each year beneath a solitary *M. glyptostroboides.* Although the long-term survival of *M. glyptostroboides* outside the boundaries of its native range is questionable, multiple lines of evidence suggest that germination and short-term establishment are possible.

3. LIFE HISTORY

Metasequoia glyptostroboides is a monoecious plant with the male (microsporangiate strobili) and female cones (macrosporangiate strobili) being borne separately on different branches of the same tree. Trees are able to produce female cones many years before they produce male pollen cones (Wyman, 1968; Kuser, 1983). Several reports suggest that viable seed are not produced until the trees reach 25 to 30 years old. This is likely a result of the absence of pollen production in younger trees. In general, trees begin producing female cones when they reach 9 to 15 m in height. I have observed trees at the Ryder's Lane Plantation, Rutgers University, New Brunswick, New Jersey producing seed cones at nine years of age (ca. 5 m tall). Male cones are typically produced when trees attain heights of 18 to 27 m.

Male cone buds are 4 to 6 mm long when closed and 6 to 10 mm long when open and releasing pollen. Mature seed cones are pendulous (with a 10- to 30-mm peduncle), and subglobose in shape. It should be noted that Li (1999) presents data indicating possible ecotypic variation in mature seed cone size in *M. glyptostroboides*. There are large (22 × 20 mm), medium (20 × 18 mm) and small (15 × 14 mm) seed cone varieties that come from trees in different positions in the landscape. Meyer (this volume) noted a size variation in fossil seed cones corresponding to different ecological and climatic settings. Cones ripen in early December and shed their seeds in late December and early January. Shao (1982) suggests that seed production begins to diminish between 40 and 60 years of age. This may have important implications for understanding the apparent lack of regeneration in many of the natural stands in China.

Across its range (natural and cultivated) pollination takes place in February or March before the tree leafs out (Fu & Jin, 1992; Hendricks & Søndergaard, 1998). An early emergence of both male and female cones may make them susceptible to late winter frosts. This may explain why some trees fail to consistently produce fertile seeds at the colder end of its cultivated range (e.g., Denmark; Vedel, 1991). *Metasequoia* apparently has some plasticity in the date at which the cones begin to develop because in many areas in North America where it is cultivated as a horticultural species the plant is producing viable seed even in areas where freezing temperatures are normal in January through March (e.g., New Jersey, Pennsylvania).

Seeds of the dawn redwood are small and light. They are approximately 5 mm long and 4 mm wide and number about 540,200/kg of seed. Germination takes about 5 to 7 days (Johnson, 1974; Williams, personal observation). Seeds sown directly on both mineral soil and potting soil (e.g., ProMix B) germinated within 7 days (Vann *et al.,* 2003). Mortality of germinants can be high in the first 5 or 6 weeks following germination. The main cause of mortality at this stage of development is damping off due to fungal attack. Seedlings are also susceptible to desiccation during this time. Vann *et al.* (2003) germinated seeds in a mist chamber programmed to deliver a 6 second burst of water every minute. Mortality of germinants after six weeks peaked at 69% even under ideal greenhouse conditions.

The natural establishment of *M. glyptostroboides* stands within its native range is poorly understood. As early as 1948, J. Linsley Gressit, who undertook an entomological collecting trip to the region, had doubts about how pristine the groves of trees growing in the Shui-sha-ba Valley really were (see Gressit, 1953). He suspected that humans had significantly altered the distribution of *M. glyptostroboides* in the valley by transplanting trees. What are believed to be naturally established stands are strongly associated with montane riparian environments and suggest that the germination and establishment of *M. glyptostroboides* is probably limited by water or substrate availability in non-riparian areas. Chu & Cooper (1950) found seedlings growing in crevices between rocks and in moist sandy places at lower elevations in ravines. Seedlings apparently also establish near natural seeps at the base of slopes. *Metasequoia glyptostroboides* seeds are small, winged, and ideal for wind dispersal (Li, 1999). Thus, the regeneration characteristics of *M. glyptostroboides* seem ideally suited for exploiting recently deposited barren fluvial sediments that would be common in its native habitat. During a field trip to the Shui-sha-ba Valley in 2002, one to two year old seedlings were found in one small stand of *M. glyptostroboides*. However, no larger regeneration was observed.

The most detailed data regarding naturally established populations of *M. glyptostroboides* are presented by Chu & Cooper (1950). They surveyed a 1000 m^2 area of the Shui-Sha-ba Valley forest to assess plant species richness and importance. Figure 9-4 presents their published diameter size class data for *M. glyptostroboides* expressed as a size frequency diagram. Based on their data, total stem density of *M. glyptostroboides* equaled about 620 stems ha^{-1}. However, 53% of the *M. glyptostroboides* were in the less than 2.5 cm diameter size class. The density of trees in the size classes that are likely to

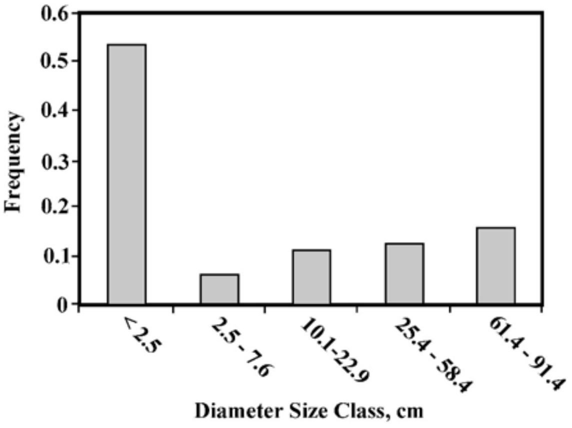

Figure 9-4. Size frequency diagram for *M. glyptostroboides* surveyed in a 1000 m^2 in Shui-sha-ba Valley, Lichuan County, China in 1950. Raw data are those of Chu & Cooper (1950).

represent overstory trees (25 cm to 91 cm) is much smaller (180 stems ha^{-1}). The picture that emerges is one of sparsely distributed larger (and older) trees mixed with a high density of very young small trees. Assuming that diameter is a good proxy for age (c.f. Williams *et al.,* 2003), these data are characteristic of an uneven age population of *M. glyptostroboides*. This is surprising given that *M. glyptostroboides* does not appear to regenerate well in the shade of other trees (Vann *et al.,* 2003).

The presence of young trees lead Chu & Cooper (1950) to believe that *M. glyptostroboides* would maintain itself as an important member of the forest community. However, others later reported that there was little in the way of regeneration in the *M. glyptostroboides* stands (Bartholomew *et al.,* 1983). Three separate stands visited by the author in 2002 during the field trip to the Shui-Sha-ba Valley all lacked small (and presumably young) trees. These observations suggest that environmental changes have occurred that have reduced the recruitment of young *M. glyptostroboides* into the larger size classes. Bartholomew *et al.* (1983) described many of the stands as being devoid of the thick understory thickets described by Chu & Cooper (1950). It is possible that human activity has resulted in decreased seedling establishment in the stands. As described above, seedlings are sensitive to moisture availability and it is possible that the more open nature of the understory may have alter the microclimate of the forest floor resulting in lower soil moisture contents and higher soil temperatures. Regardless of the cause for reduced natural regeneration of *M. glyptostroboides*, it appears that planting by humans may be the only feasible method of maintaining populations in the native range at this time.

4. GROWTH RATES AND TREE FORM

Metasequoia is a fast growing plant that attains diameters in excess of 2 m and tree heights up to 51 m in its natural range. Under ideal conditions during cultivation, *M. glyptostroboides* can attain impressive heights in relatively short time periods. Measurements of tree height reveal that *M. glyptostroboides* can attain average stem lengths greater than 30 m in less than 50 years in some parts of Europe, North American and Japan (Haupthoff, 1998; Williams *et al.,* 2003). Others report similar age but shorter trees growing in the Czech Republic, the Netherlands and Denmark (Goudzwaard & Schmidt, 1992; Hendricks & Søndergaard, 1998; Liao & Podrásky, 2000).

Based on measurements of *M. glyptostroboides* growing in plantations, it appears that most of the height growth occurs early in stand development with vertical extension slowing through time. For example, average annual height increments of 86 to 103 cm yr^{-1} have been reported for 17 to 20 year old trees in Japan (Satoo, 1974; Ikeda, 1980). These same trees measured at 48 years had reduced their vertical growth to between 48 and 56 cm yr^{-1}(Williams *et al.*, 2003). These rates of vertical growth tend to be slightly higher than European *M. glyptostroboides*. For example, Goudzwaard & Schmidt (1992) report height growth rates of 40 to 60 cm yr^{-1} for 22 to 30 year old trees in the Netherlands. Haupthoff (1998) reports vertical rates of extension for a *M. glyptostroboides* plantation in Germany of 93 cm yr^{-1}during the first 28 years of stand development and then a decrease to 31 cm yr^{-1} between 28 and 40 years. Similar rates are also noted for *M. glyptostroboides* in the Czech Republic by Liao & Podrásky (2000) who report growth rates of 67 cm yr^{-1} from 4 to 22 years old and then a decrease to a current rate of ca. 30 cm yr^{-1}.

The height of the large diameter trees in the native population is variable. Kuser *et al.* (1997) report that the mean tree height of 52 trees in the native population was 35 m with a range from 19 to 51 m. Unfortunately, the age of these trees is poorly understood due to a lack of complete annual increment cores. Estimates for the age of larger trees in the Shui-sha-ba Valley are in the 200 to 300 year old range. In general, the height growth of *M. glyptostroboides* decreases logarithmically with increasing age. Using measured changes in height through time for *M. glyptostroboides* growing in plantations as a model, we can calculate an independent estimate of tree ages if we predict the ultimate height of trees that are 200–300 years old. Using these relationships, the calculated age estimates of the larger trees in the valley corresponds closely to the previously estimated ages of 200 to 250 years (Williams, unpublished data).

Not all *M. glyptostroboides* trees grow to the great heights attained by trees in the Shui-sha-ba Valley. In some cases, *M. glyptostroboides* may develop a

Figure 9-5. Fifty-one year old (in 2001) *M. glyptostroboides* growing on Japonski Island near Sitka, Alaska. The tree is ca. 4 m tall and 33 cm in diameter.

stunted or shrub-like form, particularly in areas with relatively low growing season heat sums.

For example, Satoh (1999, unnumbered plate, p. 74) presents a picture of a *M. glyptostroboides* growing in Montreal, Canada that has bush-like or shrub-like appearance. A 51 year old *M. glyptostroboides* growing on Japonski Island in Sitka, Alaska has a very similar growth form (Figure 9-5). This tree was one of about 200 trees distributed across Alaska by B. Frank Heintzleman of the U.S. Forest Service, who later became territorial governor. Fred Geslin planted the tree, then the Assistant Superintendent of the Alaska Native Service. Geslin received 10 trees in 1950 from Heintzleman; one remains living whereas most of the others died very soon after planting (Harris, 1973; James M. Russell, personal communication, 9/2001).

The surviving tree has a similar morphology to that of the Montreal *M. glyptostroboides*. At the age of 51 years it has an overall height of ca. 4 m and a diameter at breast height of 33 cm (Figure 9-5). It has extremely dense branching that gives the plant a Krumholz-like morphology. It is also located in a fairly exposed location adjacent to Sitka Channel, which may have something to do with its shape. The tree receives an annual heat sum of 896 growing-degree days, but seldom experiences extremely cold temperature due to the moderating effect of ocean. Interestingly, a 13 year old tree planted in sheltered location near the Sitka Hospital has eclipsed the 51 year old tree in height having reached 5.8 m in October 2001 (Figure 9-6). This suggests factors other than just low heat sums may be at play in driving the morphology of the 51 year old tree.

Figure 9-6. A 13 year old *M. glyptostroboides* growing near the Sitka Hospital in Sitka, Alaska. The tree is 5.8 m tall.

Moreover, not all *M. glyptostroboides* trees have this stunted growth form in cold environments. For example, two trees growing in St. Petersburg Russia at the Komarov Botanical Institute have a relatively normal appearance, despite accumulating one-third less growing degree days than the tree in Montreal (Figure 9-7). Again, it is unlikely that temperature or heat sums alone explains this unique growth morphology.

Kuser *et al.* (1997) described genetic properties and growth data of offspring of seed collected from 20 different plants grown in a common garden experiment at the Ryder's Lane Plantation, New Brunswick, New Jersey (see Kuser, this volume for additional details). A similar set of seedlings was established at the Dawes Arboretum, in Newark Ohio. Among other things, Kuser (this volume) reports that noticeable morphological differences began to appear in the seedlings almost immediately. Based on recent sampling of the Ryder's Lane Plantation (C. Williams, unpublished data) and the Ohio plantation (M. Popovich, unpublished data) it appears that those morphological differences have persisted after 11 years of growth. For example, Kuser *et al.*

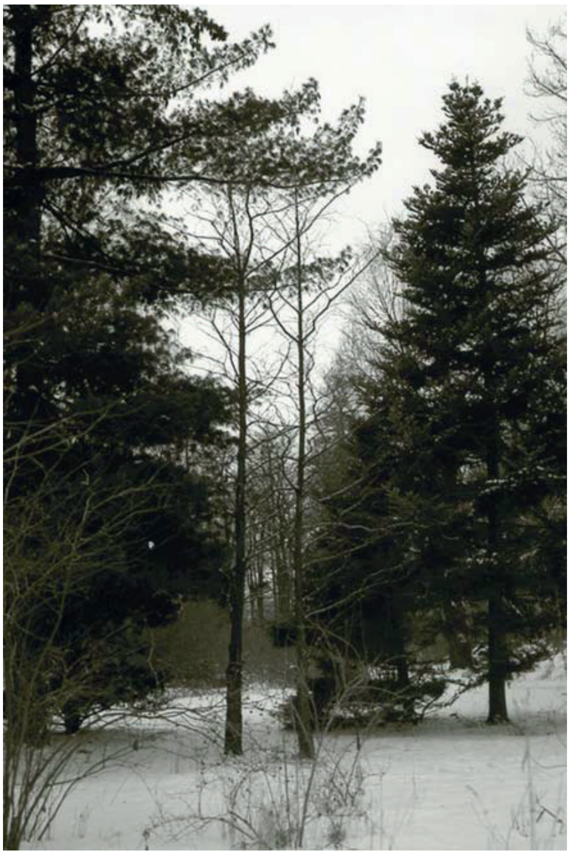

Figure 9-7. Two 49-year-old *M. glyptostroboides* (leafless-stems in center) growing at the Komarov Botanical Institute Arboretum, St. Petersburg, Russia. Photo by B.A. LePage.

(1997) ranked tree performance in terms of tree height after 4 growing seasons and described plants from seed lot #47 as slow-growing and large needled. In a general comparison, trees from seed lots 47, 7 and 50 were generally shorter than trees from other seed lots.

In my re-analysis of the same trees I found that this pattern still holds true (Figure 9-8). At the Dawes Arboretum, the trees in seed lot 47, 7 and 50 were still the shortest trees in the test plot. At the Ryder's Lane Plantation a similar pattern exists. The fact that trees from these seed lots grew slower than others, regardless of location may relate to an underlying genetic cause. Another interesting trend to emerge was that the Rutgers trees are larger in diameter than the Dawes Arboretum trees. Across all seed lots, the trees in New Jersey were significantly larger ($t = 5.110$; $p < 0.001$) in diameter (mean = 10.0 cm ± 0.28 SE) than trees in Ohio (mean = 7.9 cm ± 0.29 SE).

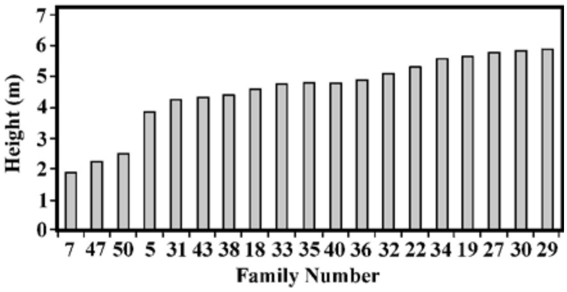

Figure 9-8. Height of 11 year old offspring from 20 different seed lots of *M. glyptostroboides* growing in a test plot at the Dawes Arboretum in Woster, *Ohio*. Data from M. Popovich (unpublished)

This may reflect the shorter growing season and slightly drier conditions in Ohio.

5. REACTION TO COMPETITION

Nearly everything we know about *M. glyptostroboides* response to competition comes from the study of plantation trees or is inferred from physiological traits (see Vann, this volume). In its native range, large *M. glyptostroboides* occur as a canopy emergent species rising above the surrounding vegetation. This is consistent with its growth characteristics such as rapid shoot elongation, rapid juvenile growth and indeterminate growth (Jagels & Day, 2003). In monospecific stands of *M. glyptostroboides*, canopy closure occurs rapidly, usually in 10 to 14 years depending on stem density (Williams *et al.*, 2003). As a result, light levels can be extremely low under intact *M. glyptostroboides* canopies (Vann *et al.*, 2003). There are two important consequences of this: (1) low

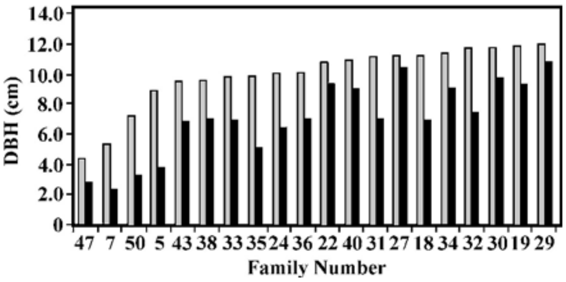

Figure 9-9. Diameter at breast height (DBH) of 11 year old offspring from 20 different seed lots of *M. glyptostroboides* growing in a test plot at the Dawes Arboretum (solid bars) in Wooster, Ohio and at the Ryder's Lane plantation (hollow bars) in New Brunswick, New Jersey. Ohio Data from M. Popovich (unpublished)

light levels tend to exclude other rapidly growing shade intolerant species from competing with *M. glyptostroboides* and (2) light levels would be low enough to inhibit *M. glyptostroboides* from regenerating under its own canopy.

Metasequoia glyptostroboides does have a unique photobiology (see Jagels & Day, 2003; Vann, this volume) for a tree that, ecologically, behaves as a shade intolerant plant. It is capable of photosynthesizing at relatively low light levels yet it does not tolerate suppression like most shade tolerant plants. *Sequoia sempervirens* (D. Don) Endlicher can tolerate suppression in the understory for long periods of time (greater than 100 years) and then accelerate growth when released. *Metasequoia glyptostroboides* does not exhibit this type of tolerance. Once suppressed, *M. glyptostroboides* appears unresponsive to increased light levels and does not accelerate growth. Observations of tree demography in high-density plantings (10,000 stems ha^{-1}) show that *M. glyptostroboides* undergo self-thinning as suppressed individual eventually die in the understory (Williams *et al.*, 2003).

6. SUMMARY

Metasequoia glyptostroboides is a unique conifer. It is a species that has undergone considerable range contraction. Despite the relatively narrow range of climate found in its natural range, it is tolerant of a wide range of climate conditions when cultivated. Its growth beyond its natural range appears to be limited by low growing season water availability and extremely cold temperatures. Many questions remain unanswered regarding the original structure and composition of pristine *M. glyptostroboides* forests. Given the degree of human land use and land cover change that has occurred in its native range it will be difficult to unravel the confounding effects of human activity on the ecology of this species. Pressing areas to focus future work on involve (1) understanding the natural controls on *M. glyptostroboides* regeneration and how to stimulate the establishment of wild populations within its native range, (2) understanding the past distribution of *M. glyptostroboides* in China in order to understand the interaction between human land use and vegetation and (3) continued monitoring of the growth of *M. glyptostroboides* within its native range and beyond to better understand the natural variation in growth rates and ecological tolerances of the species.

7. ACKNOWLEDGEMENTS

I wish to thank John Kuser for access to the Rutgers plantation and Barth Hamberg for help in locating and sampling the Sitka, Alaska dawn redwood.

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Chapter 10

Physiological Ecology of *Metasequoia glyptostroboides* Hu *et* Cheng

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Abstract: Morphologically identical representatives of the modern taxon *Metasequoia glyptostroboides* Hu *et* Cheng have been found as fossils in many Northern Hemisphere locations, indicating that since its origin in the Late Cretaceous, the genus has migrated throughout the Northern Hemisphere, and at times had a range extending over some 40 degrees of latitude. Today, the taxon is found only in a restricted area in southern China; however, it has been disseminated widely as a horticultural curiosity, and grows successfully in a variety of modern habitats. This paper examines the modern species' autecology, focusing on gas exchange relations, to address the role of physiological constraints in range contraction over time. Examination of CO_2 uptake and transpiration in response to light, temperature, humidity and CO_2 concentration indicate that *M. glyptostroboides* is drought-intolerant, adapted to low light levels and relatively cool climates, as might be expected in foggy coastal or riparian habitats. The gas-exchange relations of the modern species are sufficiently flexible to explain the presence of fossil *Metasequoia* Miki at all known sites, based on paleoclimatic reconstructions, implying that the species has not undergone any major adaptive changes in its core physiological processes. In spite of its horticultural popularity, there has been relatively little quantitative physiological examination of this species. This paper attempts to summarize what is available in the literature, providing an additional perspective on the species autecology in the context of species migration and habitat selection. *Metasequoia glyptostroboides* is shade-intolerant, germinates best on open soils, intolerant of high light levels and resists pests and disease well due to the accumulation of toxic secondary compounds. Finally, the role of *M. glyptostroboides*' deciduous habit is discussed with reference to adaptation to high-latitude photoseasonality.

Key words: autecology; deciduousness; evolutionary stasis; habitat preference; physiological adaptation; range contraction; species migration.

1. INTRODUCTION

According to reconstructions of fossil plant distributions, species of the genus *Metasequoia* Miki dominated the high latitude floras of the Northern Hemisphere during the Late Cretaceous and early Tertiary (Tidwell, 1998; LePage *et al.*, this volume). By Oligocene time a few *Metasequoia* fossils are reported from these latitudes, although they are found around the globe at lower latitudes. Between the Miocene and Pliocene, the range of *Metasequoia* shrinks further, apparently in response to climate change (LePage *et al.*, this volume). The plant fossil record is currently inadequate to map the migration of the genus accurately during this period, although refugia likely existed in southern Japan during the Pliocene (Yang & Jin, 2000; Momohara, this volume). Today, relic populations of *Metasequoia glyptostroboides* Hu *et* Cheng can be found in small areas in China (Bartholemew *et al.*, 1983).

Known initially only as a fossil, *M. glyptostroboides* (Dawn redwood) was found to be living in Hubei and Sichuan Provinces in China in the 1940's (Hu, 1948), creating some stir in the scientific community at the time (Chaney 1948; Merrill, 1948). Resultant expeditions to these restricted populations in China in the late 1940's brought specimens and seeds to the United States under the auspices of the Arnold Arboretum (Boston, Massachusetts). These seeds were subsequently distributed to institutions worldwide; additionally, Chinese scientists also sent specimens to colleagues in Europe around this time (Satoh, 1999).

Today, the oldest known specimens outside of China are those grown from Merrill's seed dissemination just over 50 years ago and these plants now live in a variety of climates. Since being introduced to horticulture in the early 1950's, the dawn redwood has proven to be a popular ornamental tree, planted around the world for horticultural qualities such as novelty, form and autumn coloration. As a result, *M. glyptostroboides* exists today in diverse environmental settings. This circumstance presents an unusual opportunity to examine some ecological, paleobotanical and evolutionary questions (see Williams, this volume).

Based on the relative abundance of fossil remains, *Metasequoia* appears to have dominated certain High Arctic environments during the mid-Tertiary (Basinger, 1991; Tidwell, 1998; Yang & Jin, 2000). These environments were characterized by permanent water such as riparian banks, flood- and braid-plains and swamps, although this could be a consequence of preservational biases (Schoenhut, 2003). In any case, understanding the physiological characters of the modern species and how they relate to both the Chinese refugia and the larger range of potential environments may provide insight into the nature of the probable climate in the high latitudes during periods in the Earth's history. The current climate of the refugia may represent a reasonable analogue of *M. glyptostroboides* paleoenvironmental settings, however physiological adaptation cannot be ruled out *a priori*.

Compared with the lower latitudes, the Arctic latitudes experience a very different annual light regime, characterized by continuous light during much of the growing season and a prolonged period of dark and low light during the dormant season. The current relic populations of *M. glyptostroboides* are located considerably below the Arctic Circle (about 30°N latitude). Therefore, did their migration require adaptational changes to the sub-arctic light patterns? Presumably, changes in daylength could affect phenological processes, and exposure to continuous daylength may have produced adaptations to the photosystem parameters to handle the stress (Jagels & Day, 2003).

Additionally, *M. glyptostroboides* has a seasonally deciduous habit. One physiological explanation for the origin of deciduousness that has been proposed suggests that the trait evolved above the Arctic Circle in response to light/dark seasonality (Axelrod, 1984; Read & Francis, 1992). These authors postulate that, for dark season temperatures above 0°C, the carbon lost from leaf tissues during dark-season respiration exceeds the cost of replacing the tissues annually, thus providing a selective pressure for deciduousness.

In spite of the horticultural popularity of the dawn redwood, very little information on the physiological characters of the species has been published. The following section summarizes or presents most of the available data on physiological characters of *M. glyptostroboides*.

2. MATERIALS AND METHODS

Gas exchange was measured using a portable photosynthesis and transpiration measurement system (LCA-4+PLC4B cuvette; Analytical Development Company, Ltd., Hertfordshire, England, UK). Calibration checks were performed before each use using a standard gas of known CO_2 concentration. Cuvette light intensity was regulated using 15 cm diameter Tiffen brand neutral density filters placed over the cuvette in full sunlight or by the LCA-4's built-in light and neutral density filters when in the lab or under overcast conditions. The LCA-4's built-in controls were also used to set humidity, CO_2 and temperature (15–40°C) levels. Temperature response below 15°C required additional cooling and was assessed in the laboratory. Laboratory measurements were performed on branches cut early in the morning and re-cut immediately under water. Branches were cut from trees at the University of Pennsylvania campus or from the Morris Arboretum, Philadelphia, Pennsylvania, U.S.A.

Field measurements of photosynthetically active photon flux density (PPFD) and temperature (ca. 15–35°C) response were conducted at eight arboreta or educational institutions spanning 30–40°N latitude using mature trees from the 1948 plant distribution (Wyman, 1970) or their vegetatively propagated offspring (see Vann *et al.*, 2003 for details). Typically, there was a single tree at each site. Three to six shoots on at least two branches on each tree were used for measurements of photosynthesis and transpiration.

Additional characterization of the light and temperature responses, as well as measurements of CO_2 and humidity response, were performed on trees at or samples from the Morris Arboretum (seven trees) or the University of Pennsylvania (two trees). Measurements were performed on days with a PPFD of at least 1500 μmole m^{-2} s^{-1}.

Carbon dioxide evolution during dark respiration was measured after completely covering the cuvette with foil. Measurements were performed in the field and laboratory at 15, 25 and 35°C; additional measurements at 5 and 40°C+ were only tested in the laboratory. Measurements were taken after the readings became steady and consistent, typically 15–25 min. Values were obtained from the average of three outer canopy leaves from each of four trees at the Morris Arboretum and from branches collected at the arboretum (six) and from the University of Pennsylvania campus (two) measured in the laboratory. Thus, n = eight for temperature values of 5 and 40°C+ and $n = 12$ for all other temperatures.

3. GAS EXCHANGE

Gas exchange, principally carbon dioxide and water, is one of the more easily determined, but vital aspects of plant metabolism. Characterization of metabolic responses to light, temperature and CO_2 concentration provide important insights into the nature of the species' optimal environment and range of tolerance. Carbon dioxide exchange reflects the balance between the fixation of CO_2 during photosynthesis (the gross carbon gain of the plant) and the loss of CO_2 during respiration. The balance is the net carbon gain of the plant, observed in biomass accumulation and turnover of deciduous tissues. Plants will be marginalized in environments that limit the potential for carbon uptake. Transpiration reflects the balance between the water status of the plant and oft-conflicting needs of maximizing CO_2 exchange while minimizing water loss and thermal loading.

The discussion below focuses on the response of net apparent photosynthesis, as determined by the uptake of CO_2, to variations in light, temperature, humidity and CO_2 concentration in the air. The temperature response of respiratory carbon losses, evaluated as dark respiration, is also examined. Other factors may influence respiration; however, these have not been evaluated for *M. glyptostroboides* at this time. The data on gas exchange presented here is that of the author. Details of the method and plant specimens used are given at the end of the chapter. Aspects of this work have also appeared previously in Vann *et al.* (2003).

3.1. Response to Light Intensity

3.1.1. Carbon Dioxide

As the energy source for photosynthesis, light intensity is a crucial factor in determining rates of carbon fixation. Because the plant photosystem only responds to a portion of the light spectrum, measurements of photon flux are confined to these wavelengths, producing a quantity referred to as PPFD (μmol m^{-2} s^{-1}). Light intensity may be expected to produce different responses in a leaf depending on whether it developed in an open or shaded environment (e.g., see discussion in Fitter & Hay, 1981). In *M. glyptostroboides*, shoots that develop on the shaded inner branches of the canopy ('shade') respond similarly to those that develop on the outer, exposed branches ('sun'); however, the 'sun' shoots demonstrate much higher uptake values at all but the lowest levels. The CO_2 uptake rate in the 'sun' shoots of *M. glyptostroboides* saturates at approximately 700 μmol m^{-2} s^{-1}; at this intensity, the rate is about 60% higher than in the 'shade' shoots (Figure 10-1). This PPFD is relatively low, about one-third of that seen on a typical clear day in the temperate zone. For both the sun and shade shoots, the uptake rate is highly sensitive to small changes at low light levels, reaching 50% of the light saturated value at only 150 μmol m^{-2} s^{-1}, although the carbon gain is trivial below 100 μmol m^{-2} s^{-1}. Following Leverenz (1987), the convexity (θ) of the light response

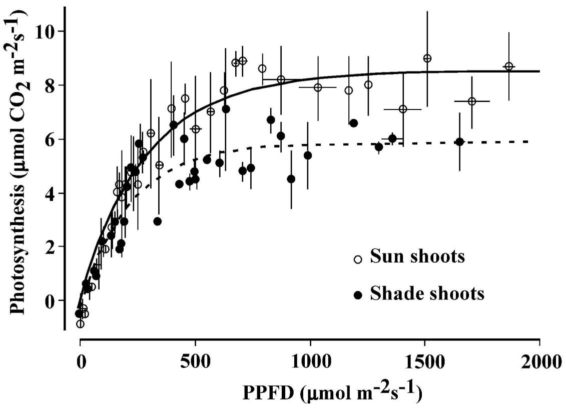

Figure 10-1. The carbon dioxide uptake in response to photosynthetically active light intensity (PPFD). The dashed line is the curve fit to the 'sun' data: $CO_2 = 8.45 \pm 0.25 \bullet (1 - e^{-0.0035 \pm 0.0003 \bullet \mathrm{PPFD}})$ $R^2 = 0.95, p < 0.0001$ model s.e.e. = 0.708. The dotted line is the same for the 'shade' data: $CO_2 = 5.87 \pm 0.29 \bullet (1 - e^{-0.0044 \pm 0.0007 \bullet \mathrm{PPFD}})$ $R^2 = 0.84$ $p < 0.0001$ model s.e.e. = 0.876. (The curves represent a mathematical model and do not indicate a biological relationship.)

curve can be calculated for the shoot. The value, 0.9, is high compared with many needle-leaved conifers (0.44–0.58), but is consistent with the planar nature of *M. glyptostroboides* shoots and the species observed shade intolerance (e.g., Kuser, 1999). Light levels decline as much as 90% below the canopy of *M. glyptostroboides* plantations (Vann *et al.*, 2003), indicating that the canopy can be a very efficient light filter, consistent with the low light saturation values seen. No significant differences in the light response curves were seen across the latitudinal range of the field measurements (data not shown).

The rapid response to low PPFD intensities suggests that *M. glyptostroboides*' optimal environment is characterized by low, diffuse light levels such as those observed in foggy or misty areas. The low light saturation value definitely indicates that the photosystem is unable to utilize fully the light intensities seen in the lower latitudes.

It should be noted that, at the extremes, the 'sun' shoot morphology tends to be dominated by thinner needles (1.5–2.5 mm wide), greater spacing between adjacent needle edges (1–1.5 mm) and longer shoots than is seen in the 'shade' shoots (needle width 2–2.5 mm, spacing 0.5–1.0 mm). Within the tree canopy, these forms intergrade. The extreme morphologies were selected for this study. Presumably, narrower needles reduce the thermal loading of shoots and canopy boundary-layer thickness. This variation in morphology as a function of light intensity was also reported by Ida (1981a), who found that the specific leaf area ("dm^2/g") increased as the light intensity decreased, whereas leaf weight remained unchanged across the gradient. A practical result of this relationship is that the light-saturated rates of carbon fixation do not differ between the 'sun' and 'shade' shoots when evaluated on the basis of dry weight rather than area.

3.1.2. Transpiration

Although transpirational water loss is a necessary consequence of carbon dioxide uptake, it also aids in the transport of nutrients from the root to shoot and effects cooling of the leaf. The balance between minimizing water loss and maximizing CO_2 uptake regulates the stomata. One consequence of this relationship is that plants tend to use less water as CO_2 levels rise and more as they decline. However, transpiration also balances the water status of the plant with the need to control leaf temperature. As long as there is an adequate water supply, transpiration can reduce leaf temperature appreciably through evaporative cooling. As the plant water status declines, so does transpiration, leading to wilting, as well as possible photo-oxidation and thermal damage to tissues.

In *M. glyptostroboides*, transpiration rates appear to double as PPFD increases from zero to about 600 µmol m^{-2} s^{-1} (Figure 10-2). In the 'sun' shoots, transpiration rates appear to peak and decline slightly, whereas the 'shade' shoots appear to remain the same or increase. However, none of these apparent trends are statistically significant using the current data set. Water loss during the dark respiration tests amounts to 0.5–1.5 mmoles m^{-2} s^{-1} (data not shown). The data indicate that the stomata open fully at low PPFD and may not respond further to intensities above those that saturate the carboxylation

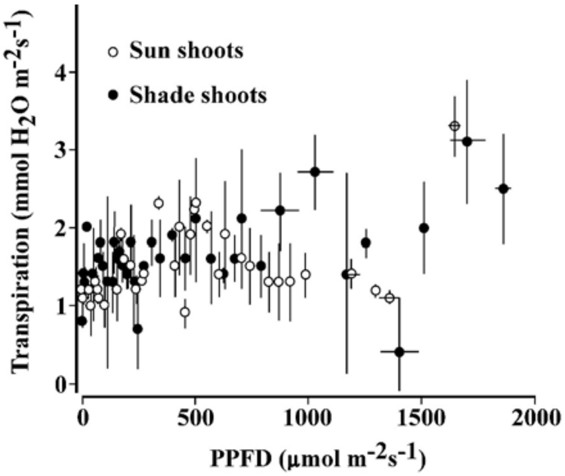

Figure 10-2. The transpiration rate of *M. glyptostroboides* across a gradient of light intensity measured as PPFD. The bars represent one standard deviation.

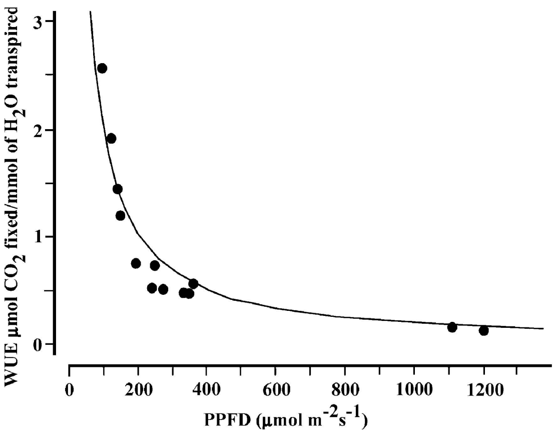

Figure 10-3. Water-use efficiency as a function of light intensity. The solid line is the curve fit to: WUE = 208/(PPFD + 0.8); $R^2 = 0.88$, $p < 0.001$ model s.e.e. = 0.246.

processes (ca. 700 µmol m^{-2} s^{-1}; Figure 10-1). Unlike the pattern seen for photosynthesis, transpiration does not appear to be different between the sun and shade shoots.

Comparing rates of carbon gain to water loss (Figure 10-3) provides an estimate of the water-use efficiency (WUE) of photosynthesis. Over a range of 300 µmol m^{-2} s^{-1} PPFD, WUE declines substantially. Above the CO_2 PPFD saturation value, there is little change in WUE, consistent with both processes being light saturated. *Metasequoia glyptostroboides* tolerates a substantial rate of water loss at PFFD values typical of any environment; WUE values near 0.5 imply a loss of 2000 moles of water for each mmole of CO_2 fixed. The WUE range for typical C3 plants is about 0.4–1.24 (Nobel, 1991), so *M. glyptostroboides* is at the low end of the range. The high transpiration rates could place a substantial demand upon soil water, so this species would not be expected to be competitive under xeric or drought conditions.

These data largely come from measurements performed in the field where complete control of each parameter was not generally possible. Temperature and humidity affect measured rates of transpiration (Kramer, 1983) and may account for much of the variability seen in the light response. Very high rates associated with a high PPFD are, at least in part, a consequence of the associated high temperatures.

3.2. Response to Temperature

Photosynthesis, as evaluated by net CO_2 uptake, shows a fairly broad response to temperature, with maximal values between 15°C and 25°C (Figure 10-4). Based on the general pattern of data, it appears that the optimal

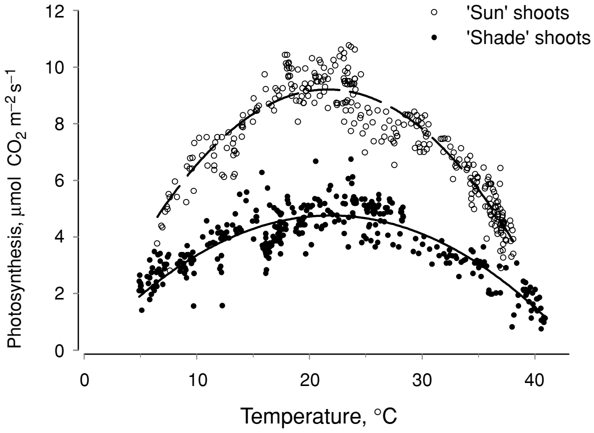

Figure 10-4. The net carbon dioxide uptake in response to temperature. The dashed line is the curve fit to the 'sun' data: $CO_2 = 0.0197 \pm 0.0002 \bullet {}^\circ C^2 - 0.852 \pm 0.006 \bullet {}^\circ C$, $R^2 = 0.877$ $p < 0.0001$, model s.e.e. = 0.673. The solid line is the same for the 'shade' data: $CO_2 = 0.0099 \pm 0.0002 \bullet {}^\circ C^2 - 0.434 \pm 0.005 \bullet {}^\circ C$, $R^2 = 0.756$ $p < 0.0001$, model s.e.e. = 0.589.

temperature for photosynthesis lies between 20°C and 25°C. The outer canopy 'sun' shoots responded similarly to the 'shade' shoots, however, the 'sun' shoots demonstrated higher values of carbon uptake at all but the extreme temperatures. The peak rate seen in the 'sun' shoots is about 2.5 times the rate seen at 5°C. Net photosynthesis declines above 25°C, with one-half the maximum rate at about 30°C; above 35°C, the rate drops very sharply. Above 40°C, the shoots did not return to pre-exposure rates within one hour, implying the possibility of damage to the photosynthetic system (data not shown). This result suggests that the optimal thermal environment for *M. glyptostroboides* could be warm- to cool-temperate, consistent with the range of climate predicted from paleofloristic studies over the fossil sites' span (e.g., Tidwell, 1998). The optimal temperature range suggested by this data is consistent with the range exhibiting maximum vegetative growth reported by Konoe (1960), as quoted by Jagels & Day (2003).

3.2.1. Respiration

As with any other species examined, the dark respiration in *M. glyptostroboides* increases with temperature (Figure 10-5), yielding a respiratory quotient (Q_{10}) near 2.3. Carbon dioxide efflux integrates the energetic costs of cellular maintenance and organismal growth. Cellular maintenance activities are comprised of repair, enzyme turnover, biosynthesis, etc. Growth includes

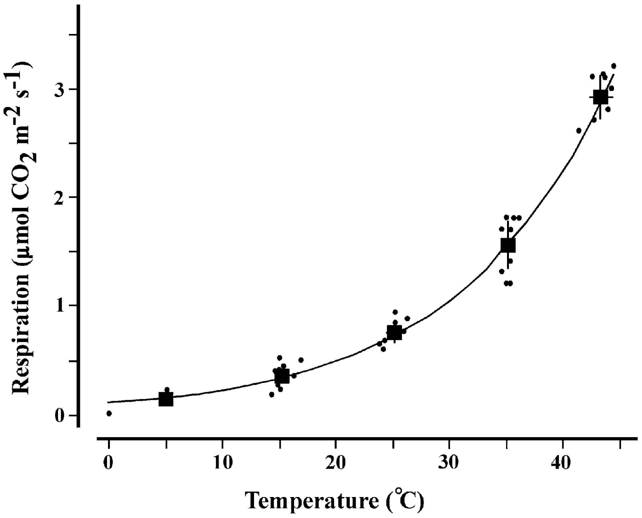

Figure 10-5. The dark respiration in *M. glyptostroboides* in response to temperature. The dots are actual data points; squares are mean value; bars are s.d.

the carbon cost of construction, which is not accounted for in CO_2 efflux from the shoots. As a consequence of thermodynamic considerations, enzyme activities generally increase with temperature up to the point of denaturation (Levitt, 1980). Concomitantly, maintenance costs increase; growth can be stimulated as well, as long as there is adequate carbon and water available. This relationship may explain why some of the highest growth rates observed in *M. glyptostroboides* occurred in well-watered individuals living in warm-temperate regions (Vann *et al.*, 2003), in spite of the apparent low net photosynthetic rates observed at the summer mean temperatures recorded for those sites. Presumably, carbon is stored during cooler months and exploited during the warmer weather.

Some of the decline in the net photosynthesis at high temperatures can be explained by the change in the dark respiration seen in response to increasing temperature (Figure 10-6). Under less-than-optimal conditions, respiratory losses could account for a significant fraction of the total carbon fixed. In ‘shade’ shoots in particular, 30–50% of the total carbon fixed is lost to shoot respiration between 30°C and 40°C. In all shoots, the respiration rates would appear to equal or exceed photosynthesis at about 40°C. Because the amount of non-photosynthetic respiring tissues (roots, stems) in a mature tree greatly exceeds the amount of shoot tissue, net carbon loss to the plant as a whole may be expected at temperatures as low as 35°C. Whole-shoot maximum carbon uptake potential substantially exceeds the potential respiration rate, suggesting that, even at high temperatures, the shoots may be net exporters of carbon.

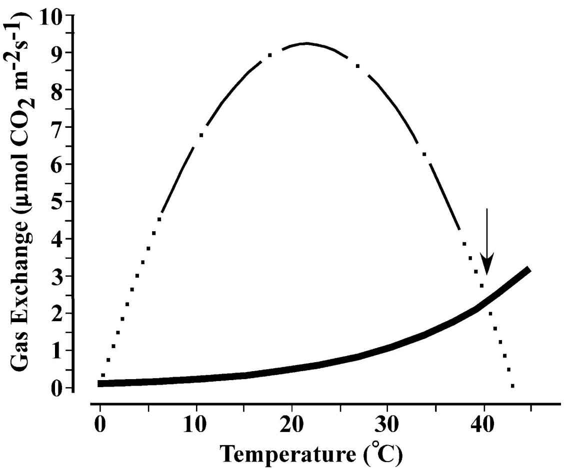

Figure 10-6. The relation between net photosynthesis and respiration. The lower curve is the respiration curve from Figure 10-5; The upper curve is the 'sun' shoot curve from Figure 10-1. The arrow indicates the point at which respiratory losses equal photosynthetic gain.

The decrease in photosynthetic rate at higher temperatures exceeds the amount attributable to respiration, as adding the respiratory losses to the net photosynthetic rate does not equal the maximum rate seen at 20°C. Temperature-driven increases in photorespiration (Grodzinski & Butt, 1977) probably account for a significant fraction of the decline; at the highest temperatures, there may direct effects on the photosystem (Levitt, 1980). Higher temperatures induce greater stomatal opening (up to a point; see below), therefore it seems unlikely that the decrease is caused by stomatal limitation.

3.2.2. Transpiration

Transpiration rates in *M. glyptostroboides* increase approximately linearly with an increase in temperature (Figure 10-7). The metabolic quotient, Q_{10}, is approximately 2.0, or slightly less at the higher temperatures. This value suggests that the transpiration rate seen in these plants is controlled primarily by diffusional processes, rather than being subject to metabolic control (Fitter & Hay, 1981), and consistent with predictions that water loss should be predictable from the energy budget of the leaf (Gates, 1968).

Transpiration rates are driven largely by the vapor pressure deficit (VPD) of the air, thus lower rates of transpiration occur at lower VPD. This can be seen in Figure 10-7, in response to controlling the relative humidity of the cuvette.

The linear increase in water loss is consistent with the result from the light-response curve (i.e., the stomata open and provide little subsequent regulation

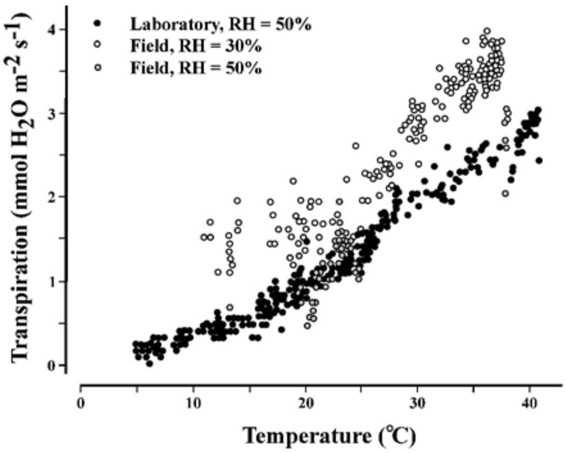

Figure 10-7. Relations between temperature and transpiration for measurements made in the field and laboratory at different VPD.

in response to temperature). Thus, water loss is not regulated directly by the stomata, even at high temperatures.

3.3. Response to Relative Humidity of Air

The highest rates of CO_2 uptake were observed at low water vapor pressure deficits, declining to about 50% of the maximum rate at around a VPD value of 5 Mpa (Figure 10-8). Measurements at low VPD (RH values above 70%) were confounded by temperature increases; although cuvette air was controlled, the

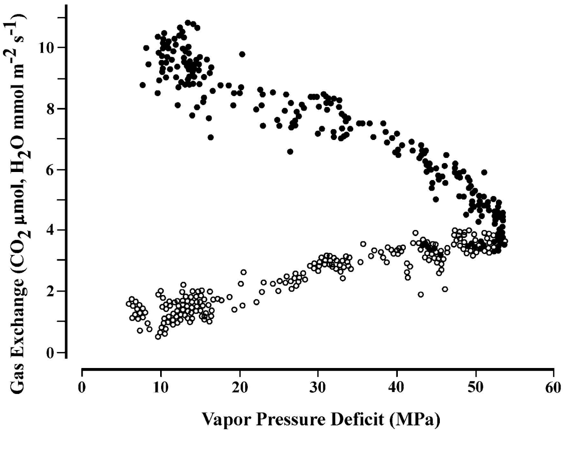

Figure 10-8. The responses of CO_2 and H_2O exchange to changes in the water content of the air at 25°C. The open circles represent transpiration; the closed circles = photosynthesis.

shoots were not able to effect evaporative cooling at higher humidity. Above about 5 Mpa VPD, carbon dioxide uptake rates become erratic and unstable. Based on instantaneous transpiration rates (data not shown), it appeared that the stomata were opening and closing irregularly, possibly in an attempt at water conservation. The rapid drop in carbon uptake above 5 MPa is accompanied by an increase in substomatal CO_2 concentration (C_i) from about 200 to 250 ppm.

As the VPD increases from < 1 to 5 MPa, water losses increase more-or-less linearly (Figure 10-8) to about three times the rates observed at 1 MPa. This is entirely consistent with the rate of water vapor diffusion expected in response to the VPD gradient. It appears that *M. glyptostroboides* reduces stomatal opening only slightly at high VPD; stomatal resistance only increases by about 20–25% over this range (data not shown). Note, however, that these plants were well watered, so the response reflects only a response to atmospheric VPD.

The decline in photosynthesis at low humidity may be partly, but not entirely due to stomatal limitation on carbon uptake. The evaporation rate under high VPD may be slightly desiccating the cells within the shoots, possibly affecting CO_2 uptake at the cell surface. This implies that even with an adequate supply of water, *M. glyptostroboides* can be expected to perform poorly in arid climates.

3.4. Response to CO_2 Concentration in Air

The atmospheric partial pressure of carbon dioxide (pCO_2) has been repeatedly shown to exert primary control of the photosynthetic rate (e.g., see discussions in Schulze & Caldwell, 1995). Consistent with the general pattern seen in C3 plants, carbon uptake declines rapidly with decreasing CO_2 concentration, reaching a projected compensation point between 50 and 100 ppm (Figure 10-9). Conversely, short-term exposure to elevated CO_2 produces a substantial increase in net apparent photosynthesis (Figure 10-9). At these high pCO_2 values, C_i is about 200 ppm below the elevated external level, indicating that carboxylation processes have not saturated.

The increase in CO_2 uptake with concentration in air suggests that the rate seen at PPFD saturation in ambient levels of CO_2 (Figure 10-1) is not primarily a limitation in carboxylation capacity, but is rather a diffusional limitation. If true, it implies that stomatal density may then limit carboxylation efficiency (on a quantum basis). This may have arisen as a compromise between water loss and carbon uptake. Xie and co-workers reported that *M. glyptostroboides* has poor drought tolerance (Xie *et al.*, 1999a, 1999b). Further experimentation is required to resolve this question. Presumably, with an adequate CO_2 supply, the light saturation value would increase, indicating that the photosystem's capacity is not saturated at current ambient CO_2 levels. This has not been tested.

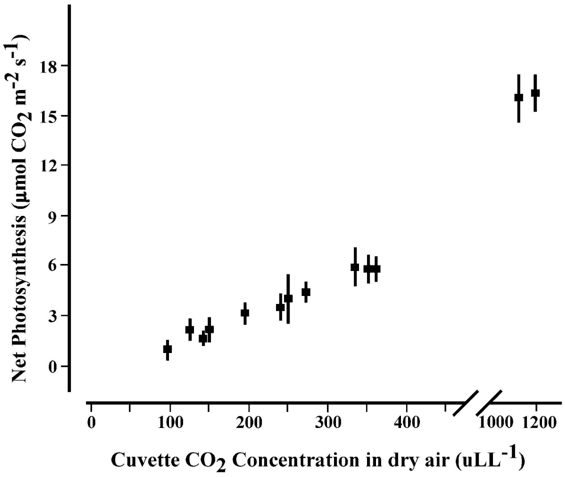

Figure 10-9. The net carbon uptake in response to carbon dioxide concentration in the air. This is a short-term response, based on the sun-type leaves. The bars represent one standard deviation.

In contrast, Osborne & Beerling (2003) report a rapid decrease in light-saturated CO_2 uptake rate in plants exposed to elevated pCO_2 over the course of a growing season simulating high-latitude light distribution, with the decline beginning with the onset of continuous light. The authors concluded that a decrease in carboxylation efficiency was responsible, ruling out photoinhibition and photodamage as possible causes. Extended exposure to high pCO_2 likely results in the production of substantial quantities of photosynthate, producing a feedback inhibition on the rate of carboxylation. However, Beerling & Osborne (2003) report that, in their saplings, total starch accumulation was only somewhat higher under elevated CO_2 conditions over the course of the simulated sub-polar summer ($p < 0.1$). This is of particular interest in examining the high-latitude physiology of the species.

Transpiration rate does not appear to be regulated by pCO_2 over the range of concentrations tested (Figure 10-10). Variability in the rate at each concentration is associated with variation among individuals and VPD (data not shown). Additional research would be needed to determine whether this species would shown an increase in WUE in response to long-term pCO_2 increases.

4. OTHER ASPECTS

Certain other physiological attributes of *M. glyptostroboides* have been published in the literature; these findings are summarized below; they

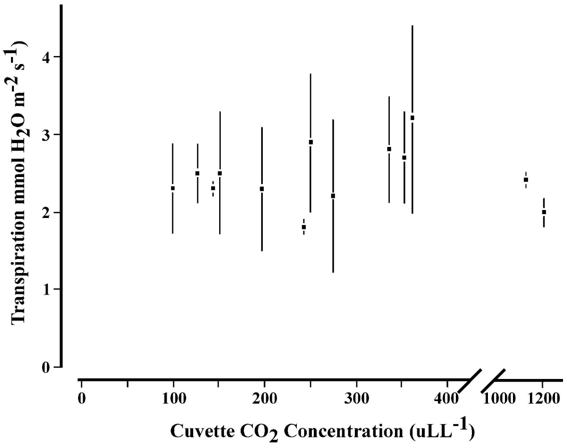

Figure 10-10. The rate of transpirational water loss at different concentrations of carbon dioxide.

include photosynthetic pigments, water relations, winter tolerance and secondary metabolism.

4.1. Pigments

Ida (1981a) reports that chlorophyll and carotenoid pigments increase and the chlorophyll a:b ratio declines with decreasing light intensity. Chlorophyll b and the carotenoids presumably act as accessory pigments in trapping additional wavelengths of light; furthermore, the carotenoids may protect the photosystem by dissipating excess energy under high light conditions or conditions inhibiting to carboxylation (see Björkman & Demming-Adams, 1995; Havaux & Niyogi, 1999). This is consistent both with general patterns seen in higher plants and with the notion that shaded leaves would be more susceptible to light damage if exposed, therefore requiring more protection. The total chlorophyll content of the 'sun' shoots in deciduous members of the Cupressaceae was higher (> 3.5 mg g^{-1}) than the evergreen members (generally < 3 mg g^{-1}); a similar pattern was seen in the carotenoid content (Ida, 1981b). Autumnal coloration characterized by reddish or reddish brown needles is widespread in the Cupressaceae, and is largely the result of the synthesis of rhodoxanthin (Ida, 1981b) and related degradation products of carotene (Czeczuga, 1987a); in the deciduous members of this family, this increase is paralleled by a sharp decline in chlorophyll and total carotene content. Rhodoxanthin production occurs commonly in the gymnosperms (with the exception of the Pinaceae); it is mostly absent in the angiosperms. The pigment may serve to protect against photo-oxidation of the photosystem during drought or cold. Leaves on young trees and upper leaves of trees in high summer sun in lower latitudes also turn red and contain rhodoxanthin (D.R. Vann, personal observation; Ida, 1981b; Czeczuga, 1987b).

4.2. Water Relations

Metasequoia glyptostroboides is associated with moist riparian habitats in its modern, relic range (Chu & Cooper, 1950) and in the reconstructed paleosites in which it has been found (Tidwell, 1998; McIver & Basinger, 1999); it achieves best growth with an adequate moisture supply (Pokorný, 1972, among others; Kuser, 1982, 1999; Bugala, 1984; Bulygin *et al*., 1990; Hendricks & Søndegaard, 1998). Besides the recognition of general drought-intolerance by several authors, Xie and co-workers (1999a, 1999b) have reported some specific characteristics of the species' water balance in several articles in the Chinese literature. In a comparison of conifers, *Pinus* L. was found to maintain cell turgor and osmotic regulation better than *Cunninghamia lanceolata* (Lambert) Hooker or *M. glyptostroboides*, with the latter ranked last (Xie *et al.,* 1999a). In a larger study comparing the relative drought tolerance of seven species, Xie and coworkers assessed *M. glyptostroboides* as being the least tolerant, co-equal with *Robinia pseudoacacia* L. Of the seven species, water stress produced the highest rates of membrane damage and lowest rates of root activity in *M. glyptostroboides*; the species ranked somewhat above the poorest species *R. pseudoacacia* in its ability to maintain water balance (Xie *et al*., 1999b). By comparison, the native range of *R. pseudoacacia* is described as humid-superhumid, cool to warm-temperate and warm-montane with mild winter (>-10°C winter minimum) appearing to grow best on moist, rich limestone-derived soils (Huntley, 1990). Data on water-stress effects on seedling establishment and growth also point to a water-sensitive metabolism (Liu & Ye, 1999).

Additionally, water stress depresses the activity of the enzymes nitrate reductase and superoxide dismutase in *M. glyptostroboides* (Xie & Shen, 2000). The latter enzyme is responsible for scavenging excess oxygen radicals generated during photosynthesis. Nitrate reductase provides amines for amino acid synthesis from nitrate absorbed by root activity. A decline in the activity of this enzyme could be due to decreases in nitrate uptake or to a low cellular energetic status caused by the water stress; water stress has been found to depress activity in a number of enzymes (see Kramer, 1983).

Jagels *et al*. (2003) report that the maximum tracheid diameter and mean length in *M. glyptostroboides* to be 69 μm and 4.54 mm respectively, and suggest that this indicates that the dawn redwood has a hydraulically efficient xylem, contributing to its ability to grow to substantial heights (some 50 m). Although their results appear to contradict the drought-sensitive nature of the tree, it should be noted that this is only one element of the water transport chain, and was predicted from wood properties, and not tested empirically. Other aspects may affect the water status of the plant, such as the apparent lack of stomatal control noted above, or limitations on the rate of water uptake by the roots. Among the species studied by Xie *et al.* (1999b), *M. glyptostroboides* had the lowest root activity under water stress. The large tracheid sizes may also increase the water storage capacity of the trunk. Jagels *et al.* (2003) also suggested that the xylem properties could assist in relieving the build-up of photosynthate transporting sugars to sites of new shoot growth under continuous light conditions unique to the polar regions.

4.3. Winter Tolerance

The only work directly examining the winter tolerance of *M. glyptostroboides* is that of Sakai (1971), who reports winter tolerance values of −25°C to −30°C for twigs and buds. This value indicates that the tree is hardy over a fairly wide range of climates and should be hardy as far north as United States Department of Agriculture (USDA) Hardiness Zone 5a (Cathey, 1986). The most northerly trees recorded for North America are growing in Sitka, Alaska (Harris, 1973), in Zone 7a; trees in Europe have been planted at least as far north as Copenhagen, Denmark (Hendricks & Søndegaard, 1998; Zone 7b) and St. Petersburg, Russia (Bulygin *et al.*, 1989; Zone 6b). Trees in Montréal, Canada (Zone 4b) show extensive evidence of shoot loss and have a short, bushy form (B. LePage, personal communication).

In trial plantations in Bohemia, Czechoslovakia (Zone 6a), it was noted that the trees were susceptible to early frosts and frost cracking (Pokorný, 1981); similarly, increment growth analysis of a tree in St. Petersburg, Russia indicated frost susceptibility, seen as dramatically lower annual increment growth due to cold winter tissue loss (Bulygin *et al.*, 1989). In both studies, it was agreed, however, that recovery was reasonably rapid. In general, the horticultural literature is consistent in noting the susceptibility of *M. glyptostroboides* to early and late frosts in colder regions (e.g., Gilman & Watson, 1994). It appears that *M. glyptostroboides* is unlikely to be competitive in Zone 4 climates, and may not perform well in Zone 5 climates in competition with other riparian deciduous genera such as *Ulmus* L., *Salix* L., *Acer* L., etc., which typically tolerate temperatures of −40°C or less (Sakai & Larcher, 1987).

4.4. Secondary Metabolism

In addition to the primary metabolic activities surrounding growth and reproduction, plants typically generate a host of compounds providing additional functions such as pest and decay resistance or UV/high-light tolerance. These compounds may be produced constitutively, or in response to specific transgressions such as wounds. One typical response to wounding in plants is the production of ethylene, which appears to function as a signal molecule, inducing defense and repair metabolism. Ethylene response to wounding was more rapid in members of the Cupressaceae than in the Pinaceae; in particular *M. glyptostroboides* and *T. distichum* (L.) Richard responded about one-half day sooner, although the highest ethylene emission levels were observed in members of the Pinaceae (Yamanaka, 1986). This rapid response may be important in the plant's overall ability to resist pests and disease.

Horticulturally, *M. glyptostroboides* is considered to be pest- and disease-resistant (Kuser, 1982, 1983). In China, a single insect pest has been recognized as being particularly important (Liu, 1983; Xu & Liao, 1985). Quantities of several bactericidal compounds, especially aromatics, have been reported by (Zhang *et al.*, 2000). The wood is highly decay resistant (Liu *et al.*, 1978); this has been further tested and confirmed by Jagels *et al.* (2003), who note that only one of four tested fungi produced significant weight loss over a 12-week period. Presumably, this resistance is related to the composition of secondary compounds in the wood; some of these have been analyzed and characterized (Enoki *et al.*, 1977a, 1977b). These extractives were phenolics of the norlignan class; it is not known whether these are bioactive compounds. A number of proantho-cyanadins have been extracted and characterized (Stafford & Lester, 1986); these compounds are generally regarded as generalized defense compounds.

Asahi *et al.* (1984) did report anti-fungal activity for diterpenes isolated from *M. glyptostroboides* wood and leaves. Such compounds would be expected to be present in the resins generated in response to wounding, and may be in part responsible for the disease-resistance of the species. They may be present constitutively in the wood, as well. Similarly, aqueous extracts of *M. glyptostroboides* leaf litter and 'volatile' component of leaves displayed allelopathic inhibition of growth in two common agricultural species, *Triticum aestivum* L. and *Brassica chinensis* L. (Wei *et al.*, 1999).

5. SUMMARY

Based on the available physiological data, *M. glyptostroboides* can be characterized as a plant with a wide tolerance of climatic conditions. However, there are limitations. Cold-temperate climates having winter temperatures below −25°C are not favorable; neither are tropical climates. Low humidity stresses the water balance of the plant; in known natural environments, both modern and ancient, *M. glyptostroboides* is associated with wet habitats, which are unlikely to have low humidity. Thus, *M. glyptostroboides* would be expected to be found in cool- to warm-temperate climates along riparian areas and possibly coastal, foggy climates, much like *Sequoia sempervirens* (D. Don) Endlicher is today. In warm-temperate climates, most of the tree's growth would likely be restricted to the cool months, with unfavorable carbon balance during the hot summer months. Lower light levels associated with foggy climates or river valleys would not affect the plant, as it remains at light-saturated levels under most conditions.

5.1. Paleoecological and Evolutionary Aspects

5.1.1. Evolutionary Stasis

Based on the fossil record, *Metasequoia* has been divided into three species based on variations in morphotype (*e.g.* Basinger, 1981; Maslova, 2000; Stockey *et al.*, 2001); earlier reports enumerating more than twenty species were re-assigned to *M. occidentalis* (Newberry) Chaney (Liu *et al.*, 1999). These species appear to be restricted to the early and middle Tertiary. *Metasequoia occidentalis* is the dominant form throughout the fossil record (∼95 Ma), and appears to have reached a peak in distribution during the early Tertiary (LePage *et al.*, this volume). In general, the fossils are morphologically indistinguishable from the modern *M. glyptostroboides*, although Liu *et al.* (1999) concluded that the modern form is distinct. This strongly suggests evolutionary stasis, at least at the morphological level (Yang, 1999). There is some indication of minor morphological variation in the modern species, possibly representing ecotypes between the Chinese populations (Li, 1999); additionally two cuticle morphotypes have been identified (Yang, 1999; Leng *et al.*, 2001, this volume). The genetic analysis of the species indicates that the populations are reasonably diverse (Kuser *et al.*, 1997), thus there is likely adequate genetic material to respond to selective pressures, if present. The level of diversity in the genotype suggests that *M. glyptostroboides* has not experienced genetic bottlenecks during the changes in range occurring over the fossil history, in spite of an apparent severe restriction to southern Japan beginning in the Pliocene (Yang & Jin, 2000; Momohara, this volume). Consequently, the genetic complement of the modern species may well be similar to that of the fossil type.

Physiological evolution can only be inferred from the fossil record, at best. The modern species' suite of physiological characters is compatible with all known fossil habitat reconstructions. This would indicate that little or no physiological changes have occurred. In particular, the low light intensities, which saturate the photosystem of *M. glyptostroboides* would permit it to grow under the reduced light intensities seen in the Arctic. Other traits, such as non-determinate growth and high xylem hydraulic capacity may have assisted in survival under continuous light (Jagels & Day, 2003). Secondary compound production, particularly resin composition, is thought to respond to changes in insect resistance (Rhoades, 1979); a comparison between modern resin and amber from middle Eocene *M. occidentalis* indicates that resin composition has changed little (Anderson & LePage, 1995). This could indicate that the species has little capacity to change, or that there has been little selective pressure; perhaps there have been few pests successful in attacking the tree. Pest species specializing on *Metasequoia* could have arisen locally, subsequently going extinct during the various range contractions.

The strongest evidence suggesting physiological evolution lies in the low-latitude fossil distribution. From the Late Cretaceous to the Miocene, fossil *Metasequoia* have been reported from paleolatitudes around 35–40°N in the southwestern United States and in China and Japan. These paleolatitudes would have placed the fossil trees in warm-temperate – bordering on equable subtropical climates. Gas exchange measurements from the modern species suggest that these climates would be sub-optimal. It is certainly conceivable that the fossil trees may represent a warm-adapted ecotype of the modern species, perhaps with a physiological optimum resembling that of its warm-temperate relative, *Taxodium* Richard. This leaves open the question of why this lineage failed to find refugia during the Pliocene, and became extinct. At lower latitudes, the low light saturation value seen in the *M. glyptostroboides* photosystem could have affected the species' competitiveness compared with riparian angiosperms with a higher light saturation value. The species' decay and pest resistance may have permitted the tree to persist in wetter areas; the closely related genera *Taxodium* and *Glyptostrobus* Endlicher survive in saturated soils. The latter genera have root adaptations (pneumatophores) that permit them to grow in areas inundated with water; *M. glyptostroboides* lacks these and prefers somewhat drier sites. Thus, even under suboptimal warm climates, *M. glyptostroboides* may remain competitive in wet edge habitat that otherwise competitive angiosperms cannot tolerate.

During the later Tertiary, the Rocky Mountain and Himalayan orogenies probably played significant roles, altering local climate (LePage, 2003). For instance, in the Western United States, gradual drying of the terrain east of the Rocky Mountains would have confined *Metasequoia* to moist/misty mountain valleys similar to the modern sites. At lower latitudes, drier air combined with high light intensities would produce a climate in which *Metasequoia* would have likely been poorly competitive. Subsequent glaciation would have both eliminated the species from these mountain refuges and the fossil record of their presence. Conversely, low-latitude sites may have had only a small, but persistent component of *Metasequoia*, with a strong taphonomic bias in preservation due to the decay-resistance of the species (Jagels *et al.*, 2003; Schoenhut, 2003).

In any event, *M. glyptostroboides* would appear to represent as good a 'nearest living relative' of *M. occidentalis* as can be expected and may represent a morphologically and physiologically unchanged descendant.

5.1.2. Species Migration

Although *M. glyptostroboides* is successful in a variety of horticultural settings, several factors may be expected to limit its success in a similar range of natural habitats. The association between physiology and humid/perhumid mesothermal, hydric environments indicate that physiological constraints will limit *M. glyptostroboides* to a fairly restricted range of riparian habitats. This is further controlled by germination and establishment requirements; a higher success rate occurs on open substrates such as the fresh sediments that would be expected in disturbed deltaic or floodplain environments (Vann *et al.*, 2003). Riparian habitat, however, makes up only a small fraction of the available terrestrial domain, and tends to be disjunct. Thus, regional scale climatic change resulting in drier and/or colder conditions would eliminate suitable habitat, fragmenting populations.

The apparent intolerance of cold winters is consistent with the lack of fossil *Metasequoia* in the Arctic regions during the global cooling events of the Neogene (Yang & Jin, 2000). Glacial onset in the Pleistocene probably finalized the extinction of fragmented local populations of *Metasequoia*. Given that species near the edge of their range perform very poorly, it is reasonable to conclude that minimum temperatures at the Oligocene and Pliocene Arctic Circle were at least $-20°$C, as *Metasequoia* is absent above 65°N during these periods. Conversely, the warm periods during the Paleocene and Miocene see a loss of the southern extent in the United States, consistent with the lack of tolerance to high temperatures and dry conditions. This pattern is not evident in southeastern Asia during these periods, possibly due to climate-moderating influences from the Sea of Japan. Thus, the overall pattern of migration is consistent with the broad climate pattern, as the species exploits suitable habitats.

More difficult to explain through autecological analysis is the apparent disappearance of *Metasequoia* throughout the world during the Pliocene/Pleistocene (LePage *et al.*, this volume; Momohara, this volume), evident only in fossils from southern Japan. This could, of course, be an artifact of the plant fossil record. Conceivably, as discussed above, the Miocene warming relegated *Metasequoia* to cooler, upslope positions where rapid subsequent climate change associated with the onset of glaciation extirpated the montane populations and poor competitiveness against the established downslope angiosperms resulted in complete loss. The subsequent disappearance from Japan and re-appearance in the Holocene of China is, at present, unexplained.

It seems likely that, as exploration proceeds, Pleistocene fossils will be found in southern China.

5.1.3. High-Latitude Survival

The earliest known fossils described as *M. occidentalis* occur in eastern Siberia and Canada in Cenomanian age strata at paleolatitudes ranging between 70°N and 80°N in Siberia and 55°N in western Canada (LePage *et al.*, this volume). The annual light regime in the Arctic yields a light-dark seasonality that could place considerable strain on tree physiology (Jagels & Day, 2003). Although the light intensities are low, the total daily light flux seen in the high latitudes is greater than that at the lower latitudes (Vann *et al.*, 2003), a situation that could lead to photo-oxidation of the photosystem and/or accumulation of photosynthate. It may be surmised that *Metasequoia* originated below the Arctic Circle; however, its physiological characters at that time are, of course, unknown. Assuming evolutionary stasis since at least the Miocene, the characters observed in the modern species may be a consequence of adaptation to the Arctic climate or may represent characters that predated the migration though the Arctic, but may have "pre-adapted" the species for success in that environment.

Several aspects of the species' physiology are consistent with the ability to survive under Arctic conditions. The low light saturation value (Figure 10-1) is at or near light levels measured in the modern Arctic (Vann *et al.*, 2003). Xylem hydraulic properties may assist in the transport of photosynthate generated during the continuous daylight period and indeterminate shoot growth may provide both a continuous sink for photosynthate and a means to adapt morphologically to seasonally changing light levels (Jagels & Day, 2003). However, Arctic light intensities may be low enough to reduce the quantity of the 'sun' morphology foliage compared with that seen at lower latitudes; few fossil leaves resembling the 'sun' morphology are present in the preserved 45 million year old (Ma) litters at Napartulik, Axel Heiberg Island, Canadian Arctic (Schoenhut, 2003). In spite of the low intensities, shoots of plants exposed to continuous light develop a reddish color (R. Jagels, University of Maine and D. Beerling, University of Sheffield, personal communication); this color is indicative of the presence of rhodoxanthin (Czeczuga, 1987b), and probably acts as a shading mechanism to reduce the potential for photo-oxidation.

Bulk wood samples from the Eocene-age Napartulik site on Axel Heiberg Island, Canada exhibit δ^{13}C values *ca.* –20‰, compared with –28‰ for modern plants (R. Jagels, University of Maine and H. Jahren, Johns Hopkins University, personal communication). Assuming that the δ^{13}C content of the atmosphere was similar to that measured in modern air, the fossil signature suggests that these plants had a low (long-term) stomatal conductance (Farquhar *et al.*, 1989).

Partial stomatal closure may have been a mechanism to reduce the rate of carbon gain in order to balance the rate of photosynthate export from the leaf. Analysis of the middle Eocene Napartulik fossil trees indicate that they were slow-growing compared with modern *M. glyptostroboides* growing at lower latitudes, having an aboveground net primary production rate consistent with a cool temperate climate (Williams *et al.* 2003). Using the production rates from Williams *et al.* (2003) and the specific leaf area data, the average annual photosynthetic rate can be back-calculated; the values suggest that the seasonal rate was about 70% of the theoretical maximum deduced from the data above (e.g., Figures 10-1 and 10-3). This is at least consistent with the suggestion that the stomata may have remained partially closed in the trees at this middle Eocene Arctic site. Of course, reduced production rates may also be a consequence of sub-saturating light flux during periods of cloud cover.

Alternatively, Jagels & Day (2003) have suggested that continuous canopy photosynthesis may have been enough to draw down the canopy CO_2 concentration to the point where ^{13}C discrimination is reduced. However, reducing canopy pCO_2 to a level that would reduce $\delta^{13}C$ discrimination several ppt would result in pCO_2 values low enough to inhibit photosynthesis (Figure 10-9). Conversely, because the ^{13}C content of the fossil atmosphere is virtually impossible to assess using fossil plant remains (Beerling & Royer, 2002), it is possible that the fossil wood value simply indicates that the $\delta^{13}C$ value of the Eocene atmosphere was near zero.

5.1.4. Evolution of Deciduousness

The evolution of deciduousness in conifers is an intriguing phenomenon, given that conifers are successful evergreens in a very wide range of climate, from tropical to boreal, from arid to perhumid. Several hypotheses have been advanced to explain the origin of deciduousness. The extended period of darkness during the polar winter may result in an expenditure of carbon in respiration that exceeds the carbon cost of replacing foliage (e.g., Spicer & Chapman, 1990); alternately, periodic drought may have been a driving force (Axelrod, 1966); or deciduousness may be an advantage in successional environments (Givnish, 1979). Deciduousness clearly arose more than once in plant lineages, quite possibly in response to different selective pressures; it may remain as a facultative stress response in general. Certainly, leaf senescence is a common generalized response to stress; deciduousness as a synchronized response to an external stimulus represents a specific response to recurring stress, presumably correlated with some climatic signal, such as temperature or day length. Whereas generalized senescence may be sensed by leaf carbon balance, deciduousness is triggered by a specific sensor within the plant, and is presumably under selective pressure.

Cellular events prior to autumn leaf drop in *M. glyptostroboides* are notably different from the pattern seen in temperate angiosperms. Cells do not follow an orderly sequence of disassembly, instead disintegrating somewhat chaotically (Schoenhut, 2003). This pattern more resembles that of desert or tropical drought deciduous plants, which drop their leaves very rapidly with the onset of drought, leaving little time for orderly disassembly and recovery of nutrients and photosynthate. If *Metasequoia* evolved in an area experiencing seasonal drought cycles, the predictable nature of the environment may have then resulted in the evolution of a photosensitive trigger initiating leaf loss. Structured disassembly of cells allows deciduous angiosperms to recover substantial amounts of nutrients from the shed leaves; *M. glyptostroboides* does not recover a substantial nor consistent amount of nutrients from its shed leaves (D.R. Vann, unpublished data). It is possible that the plant never evolved a system for orderly disassembly, possibly because the onset of drought reduces the nutrient recovery potential, so there would be little selective pressure to do so.

Can the photosynthetic characters of *M. glyptostroboides* test the first hypothesis, that of carbon balance between respiration and leaf replacement? Certainly, plants shed leaves in shaded portions of the canopy when they have a negative carbon balance, so a mechanism exists whereby a coordinated response could evolve. Experiments using meter-tall saplings (Osborne & Beerling, 2003; Royer *et al.*, 2003) suggest that the cost of replacing the canopy greatly exceeds the cost of the canopy respiration; these authors reject the hypothesis. However, the whole-plant carbon balance of saplings is not an adequate model to test the hypothesis. The canopy-to-total respiring biomass ratio is high in young plants; they could not become established otherwise. More critical to assessing questions of the evolution or adaptive significance of deciduousness is the carbon balance of mature trees, as a tree must achieve reproductive stature before a trait is passed on. In *M. glyptostroboides*, successful sexual reproduction does not occur until the tree is some 15 meters tall. Large trees have a much greater proportion of respiring biomass in the trunk, branches and roots. Respiration consumes the majority of carbon fixed, leaving proportionally less for growth and storage. Using an oversimplified analysis, Vann *et al.* (2003) found that the whole-tree carbon balance becomes unfavorable above the Arctic Circle when the winter temperatures exceed 7–10°C. Because this temperature is probably higher than actual polar winter temperatures, the result agrees with the Royer *et al.* (2003) analysis. However, sub-optimal conditions, such as cloud cover, herbivory or other factors, including errors in the calculation due to the lack of detailed measurements on root and bark respiration may have overestimated the carbon resources available to the plants. So, the hypothesis cannot be clearly rejected based on the available evidence, however, neither is it supported by that evidence. Conversely, it may be more instructive to ask whether deciduousness evolved in response to seasonally recurring drought, might have provided *Metasequoia* with a physiological edge in the polar light climate (Jagels & Day, 2003). Wolfe (1987) provides a cogent explanation related to the terminal K/T event and the presumed subsequent impact winter, which selected for deciduous taxa. His scenario is consistent with both the suggestion that high CO_2 in the Cretaceous would have favored evergreen dominance at high latitudes (Beerling & Osborne, 2002) and the long-noticed dominance of deciduous species at high-latitudes during the early to mid Tertiary.

6. MATERIALS AND METHODS

Gas exchange was measured using a portable photosynthesis and transpiration measurement system (LCA-4 + PLC4B cuvette; Analytical Development Company, Ltd., Hertfordshire, England, UK). Calibration checks were performed before each use using a standard gas of known CO_2 concentration. Cuvette light intensity was regulated using 15-cm diameter Tiffen brand neutral density filters placed over the cuvette in full sunlight or by the LCA-4's built-in light and neutral density filters when in the lab or under overcast conditions. The LCA-4's built-in controls were also used to set humidity, CO_2 and temperature (15–40°C) levels. Temperature response below 15°C required additional cooling, and was assessed in the laboratory. Laboratory measurements were performed on branches cut early in the morning and re-cut immediately under water. Branches were cut from trees at the University of Pennsylvania campus or from the Morris Arboretum, U.S.A.

Field measurements of PPFD and temperature (ca. 15–35°C) response were conducted at eight arboreta or educational institutions spanning 30–40°N latitude using mature trees from the 1948 plant distribution (Wyman, 1970) or their vegetatively propagated offspring (see Vann, *et al.* for details). Typically, there was a single tree at each site. Three to six shoots on at least two branches on each tree were used for measurements of photosynthesis and transpiration.

Additional characterization of the light and temperature responses, as well as measurements of CO_2 and humidity response, were performed on trees at or samples from the Morris Arboretum (seven trees) or the University of Pennsylvania (two trees). Measurements were performed on days with a PPFD of at least 1500 μmole m^{-2} s^{-1}.

Carbon dioxide evolution during dark respiration was measured after completely covering the cuvette with foil. Measurements were performed in the field and laboratory at 15, 25 and 35°C; additional measurements at 5 and 40+°C were only tested in the laboratory. Values were obtained from the average of three outer canopy leaves from each of four trees at the Morris Arboretum and from branches collected at the arboretum (six) and from the University of

Pennsylvania campus (two) measured in the laboratory. Thus, $n =$ eight for temperature values of 5 and 40+°C and $n = 12$ for all other temperatures.

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Chapter 11

Competitive Advantages of *Metasequoia* in Warm High Latitudes

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Abstract: Although the fossil remains of several conifer species have been found from numerous lowland Eocene sites throughout the very high latitudes (above 75°N), many were rarities, and only *Metasequoia* Miki appeared to have thrived under the warm and unique lighting conditions of the High Arctic regions of the Northern Hemisphere. To estimate the relative competitiveness of the fossil conifers, mechanical/hydraulic stem attributes, photosynthetic water-use-efficiency and photobiology were compared among extant nearest-living-relatives: *Metasequoia glyptostroboides* Hu *et* Cheng, *Sequoia sempervirens* (D. Don) Endlicher, *Taxodium distichum* (L.) Richard, *Glyptostrobus pensilis* (Staunton *ex* D. Don) K. Koch and *Larix laricina* (Du Roi) K. Koch. Based on these physiological comparisons we conclude that *Taxodium* Richard would have been limited primarily by a significant decrease in photosynthetic efficiency when growing under continuous light. *Sequoia* Endlicher should have been highly competitive, but was likely limited by its evergreen habit. *Glyptostrobus* Endlicher would have been restricted to minor component status by its slow growth rate and short stature. Finally, although *Larix* Miller demonstrated improved water-use-efficiency under continuous light, it had a less-competitive photobiology than *Metasequoia*, and sequestered more resources into stem biomass.

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Key words: continuous-light; Eocene; hydraulics; *Metasequoia*; palaeo-ecophysiology; photobiology; stem mechanics; water-use-efficiency; wood density.

1. INTRODUCTION

By the Late Cretaceous *Metasequoia* Miki was growing between latitudes 55°N and 80°N in eastern Asia and western North America (Yang & Jin, 2000; LePage *et al.*, this volume). *Sequoia* Endlicher and *Taxodium* Richard were found at similar latitudes during this period (Aulenback & LePage, 1998; Ferguson, 1967; Florin, 1963). During the early Tertiary *Metasequoia*, became more widely distributed in longitude and occupied a greater number of sites above 70°N latitude (Yang & Jin, 2000). By the middle Eocene *Metasequoia* dominated many lowland swamp forests at the very high latitudes (at least to 80°N), where growing seasons were mild (mean annual temperatures exceeding 14°C) and winter periods were dark, but warm (Tarduno *et al.*, 1998; Greenwood & Basinger, 1994; Momohara, 1994; Christie & McMillan, 1991; Francis, 1991; Irving & Wynne, 1991; Estes & Hutchison, 1980).

Several studies have provided evidence that *Metasequoia glyptostroboides* Hu *et* Cheng has remained relatively unchanged since the Tertiary. Morphological homogeneity through time is supported by the research of Liu *et al.* (1999) and Yang & Jin (2000). Physiological stasis is more difficult to determine, but Jagels & Day (2004) and Vann *et al.* (2004) present indirect evidence. Chemical homogeneity through time is also difficult to demonstrate, but the analysis of fossil and modern amber resin of *Metasequoia* indicates chemical concurrence except what might be expected from oxidation (Anderson & LePage, 1995). Although living *M. glyptostroboides* displays a moderate level of genetic heterogeneity (Li *et al.*, 1999; Kuser, 1998), molecular testing indicates a slow nucleotide substitution rate (Yang & Jin, 2000). Even the mycorrhizal associations have remained the same for at least 50 million years (Stockey *et al.*, 2001). Finally, it should be noted that although several fossil species of *Metasequoia* have been noted in the literature, the morphological variation among those species is no greater than that found in *M. glyptostroboides* (Liu *et al.*, 1999). And since *M. glyptostroboides* is the only extant species, the evidence points to evolutionary stasis (Li *et al.,* 1999).

Based on the presumed homogeneity between extant and fossil *Metasequoia* we have been exploring the biomechanical and physiological aspects of *M. glyptostroboides*, as a nearest living relative (NLR), in order to gain insight into its adaptability to a warm high latitude environment (Jagels & Day, 2004; Jagels *et al.*, 2003). In this chapter we review some of the evidence from our previous work; but, in addition, we examine the question of why *Sequoia* and *Taxodium*, which have similar morphological characters and ecological niches, were either absent from the highest latitude paleosites or only found as rare components (Francis, 1991; Basinger, 1991; Schweitzer, 1980). Our expectation from this kind of comparative analysis is to reveal the possible limiting factors, which allowed or thwarted successful occupation by particular species in the high, warm paleo-latitudes.

Chaney (1951) examined earlier reports of the fossil remains of *Sequoia* and *Taxodium,* and re-assigned many of them to the then recently discovered genus *Metasequoia.* He pointed out the difficulty of separating these three genera from fossil remains. Based on Chaney's re-evaluations and our search of the more recent literature, we conclude that *Taxodium* has not been definitively identified in North America in the fossil record at latitudes above 51°30'N, where *T. wallisii* Aulenback *et* LePage was reported from the Late Cretaceous (Maastrichtian) of Alberta (Aulenback & LePage, 1998). Hollick (1936) reported finding Tertiary fossils of *Taxodium* from southern coastal Alaska at latitudes below 65°N (Chaney, 1951). However, these fossils have been identified as those of *Metasequoia* (LePage *et al.*, this volume). Schweitzer (1980) reports the presence of *Taxodium* from Spitsbergen, about 80°N, but only as a minor component in an early Tertiary forest dominated by *Metasequoia.*

Similarly, *Sequoia*, following re-assignment of previously identified *Sequoia* fossils to *Metasequoia*, was mostly absent from the high latitudes during the Tertiary. Chaney (1951) argues that the absence of *Sequoia* from these high latitudes provided the isolation for the development of different *Sequoia* species in Europe and North America. We found one report of the presence of *Sequoia* from a high-latitude Cretaceous (Turonian) site in Russia. Sveshnikova & Budantsev (1969) identified the species *Sequoia tennuifolia* Sveshnikova *et* Budantsev from New Siberia Island, 80°N. Schweitzer (1980) reports *Sequoia* as a minor component, together with *Taxodium* in the *Metasequoia* dominated early Tertiary forests of Spitsbergen. Neither *Sequoia* nor *Taxodium* have been reported from the highest latitude North American paleosites.

Glyptostrobus Endlicher has been reported from both the North American and Eurasian high latitudes (80°N) during the Eocene, but only as a minor component (Visscher & Jagels, 2003; Basinger, 1991; Schweitzer, 1980).

Our purpose in this study was to compare *M. glyptostroboides* with other species that were present in the Tertiary, but only those that occurred as rare and as minor components of the high latitude forests and currently have extant representatives that occupy ecological niches similar to those of *M. glyptostroboides* (Ornduff, 1998; Kozlowski *et al.,* 1991; Conner & Day, 1976; Henry & McIntyre, 1926). By comparing the physiological and biomechanical characteristics of these species we hoped to provide an explanation for why only *Metasequoia* grew as a dominant tree at many of the highest latitudes during the Eocene.

2. COMPETITION CRITERIA

The NLR species compared in this chapter are *M. glyptostroboides, Taxodium distichum* (L.) Richard and *Sequoia sempervirens* (D. Don) Endlicher. *Larix laricina* (Du Roi) K. Koch and *Glyptostrobus pensilis* (Staunton *ex* D. Don) K. Koch are also included in selected comparisons for reasons given below. All, except *L. laricina,* are members of the Cupressaceae; they all occupy wet sites and are poor competitors on better sites.

The presence of a deciduous habit might be considered a mandatory prerequisite for the highest latitudes during the warm Eocene, but fossil remains of *Picea* A. Dietrich and *Pinus* L. have been found at these paleosites at latitudes as high as 80°N, although it is most likely that these trees were growing in the colder, higher elevations since only cones, leaves and small branches are found in the *Metasequoia* dominated floodplain and swamp forest sites (Basinger, 1991; Francis, 1991; Schweitzer, 1980; LePage, 2001). We have included the non-deciduous *Sequoia sempervirens* in our comparative physiological experiments and biomechanical/hydraulic analyses, in part, to test whether the evergreen habit could be a primary limiting factor preventing high latitude adaptation of a warm temperate climate species.

Three basic lines of evidence are explored to assess the potential adaptability of *M. glyptostroboides* and its close relatives to a warm, wet, high-latitude environment where a season of total darkness alternates with a season of continuous low intensity illumination (Pielou, 1994). We will begin by examining the hydraulic/mechanical aspects of the xylem, followed by a comparison of photosynthetic water-use-efficiency (WUE) and conclude with an examination of the photobiology.

Since an adequate supply of moisture and a photosynthetic system adapted to the prevailing light regime are the two primary factors that permit plants to adapt and compete with co-occurring species (Kozlowski & Pallardy, 1997; Niklas, 1992), our analyses and experiments are focused on these features. Since trees must connect a soil moisture supply with a canopy that may be of considerable distance, the hydraulic efficiency and mechanical support are key ingredients for successful competition (Niklas, 1992). Therefore, we analyzed the stem hydraulic efficiency and mechanical support in *M. glyptostroboides* and compared it to *Glyptostrobus pensilis*, *Sequoia sempervirens* and *Taxodium distichum*. Linked to stem hydraulic efficiency is WUE. This is particularly important for conifers that normally recharge sapwood moisture at night (Pallardy *et al.*, 1995). Under continuous illumination the night recharge period is unavailable. Thus, in theory, even wet site species, might be better adapted to a continuous light (CL) environment if they have a high canopy WUE. Stem capacitance was not investigated, but for the purposes of this study we are

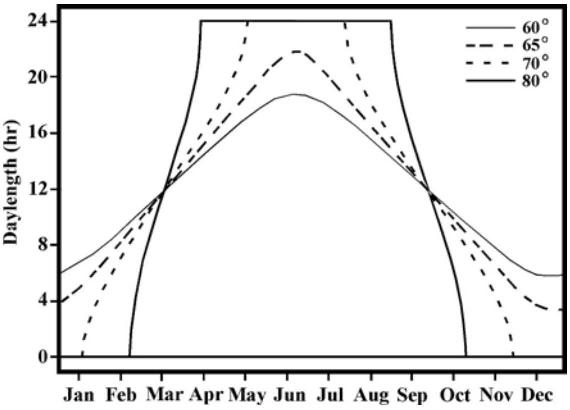

Figure 11-1. Annual light/dark regimes at 4 different latitudes.

assuming rough parity within the Cupressaceae for trees of comparable height. This may be an erroneous assumption, and should be investigated in the future.

We hypothesize that one of the most important limiting factors of the high latitudes is the unique light/temperature regime imposed during the Cretaceous and Tertiary, an ecological niche that is not currently available to modern temperate forest constituents. Any species that developed a photobiology particularly adapted to low intensity CL in a temperate climate would likely have had distinct adaptive advantages.

Several researchers have investigated the physiological ramifications for plants adapting to warm high latitude sites, in both the Northern and Southern hemispheres (Read & Francis, 1992; Beerling & Osborne, 2002). However, a broad range of "high" latitudes have been considered in these studies without clearly distinguishing the significant differences in the annual light regimes. The annual light regimes for the latitudes of 60, 65, 70 and 80°N are compared in Figure 11-1. At 60° and 65° plants are exposed to relatively long summer days and short winter days, but not to any periods of continuous light or continuous darkness. At 70° plants are exposed to less than two months of continuous light and continuous darkness. By 80° the continuous light and dark periods are each nearly 4 months in length. Plants that adapted to 80°N were clearly exposed to quite different light regimes than those that grew near the Arctic Circle (66.5°N). In this chapter we focus our attention on light regimes found above 75°N.

3. MECHANICAL/HYDRAULIC ATTRIBUTES

In Table 11-1 the physical and mechanical (columns 2–4) and hydraulic conductance (columns 5 and 6) attributes of *M. glyptostroboides* are compared with

Table 11-1. Mechanical and hydraulic properties of the xylem of selected Cupressaceae stems[1]

Species	Specific gravity[2] (SG)	MOR (kPa)	MOR (MPa)	Maximum tracheid diameter (mμ)	Approximate relative conductance
M. glyptostroboides	0.27	33,000	5,100	69	6×
G. pensilis	0.28	—		45	1×
T. distichum	0.42	46,000	8,100	70	6×
S. sempervirens	0.34	41,000	6,600	80	10×

[1] Data for *M. glyptostroboides* and *G. pensilis* from author's tests; data for *T. distichum* and *S. sempervirens* from Anon, 1999 and Panshin & deZeeuw, 1980.

[2] Green volume, oven-dry weight basis. MOR and MOE values for green wood.

those of *T. distichum*, *S. sempervirens* and *Glyptostrobus pensilis*. In conifers that have a well-defined latewood (LW), a partial division of labor can exist such that earlywood (EW) tracheids are designed primarily for hydraulic conductance and secondarily for strength while LW tracheids are designed primarily for strength and secondarily for hydraulic conductance, as is the case in many species of the Pinaceae. In these species the composite structure of alternating bands of low density EW and high density LW can develop high strength and stiffness while providing for adequate hydraulic conductance (Domec & Gartner, 2002; Tyree *et al.,* 1994; Carlquist, 1975).

In many species of the Cupressaceae, which generally lack well-defined latewood, strength may be sacrificed in order to gain hydraulic efficiency. Specific gravity (SG), except in the case of reaction wood, is generally a reliable predictor of wood strength (Jagels *et al.*, 2003), particularly modulus of rupture (MOR). A comparison of the values in columns 2 and 3 show this relationship (Table 11-1). Although we have no strength or stiffness values for *G. pensilis*, the SG value, which is nearly identical with *M. glyptostroboides* indicates that these two tree species likely have similar strength properties. *Taxodium distichum*, with the highest SG, has the highest strength in bending, as measured by MOR, and the highest stiffness or modulus of elasticity (MOE). Stiffness is related in part to cell wall microfibril angle and possibly tracheid length and so does not always show as strong a correlation with SG (Astley *et al.*, 1998; Booker *et al.*, 1998; Meylan & Probine, 1969; Carlquist, 1975; Rundel & Stecker, 1977; Wellwood, 1962).

The hydraulic conductance of a hollow capillary is proportional to the fourth power of its diameter (Zimmerman, 1983; Reiner, 1960); therefore a small increase in diameter can have a dramatic influence on conductance. Hacke *et al.* (2004) have demonstrated that tracheid length in conifers is scaled to maximize the potential of tracheid diameter. Therefore, relative conductance efficiency can be compared directly from tracheid diameter. If we use the maximum tracheid diameter of *G. pensilis* as a base value (1 ×), then *M. glyptostroboides* and *T. distichum* are approximately six times more efficient in conductance. *Sequoia sempervirens*, with the largest diameter, has a theoretical hydraulic conductance that is greater than 10 times that of *G. pensilis*.

The greater the hydraulic conductance in conifers the taller the potential height of a tree. *Sequoia sempervirens* has the largest diameter tracheids of any Northern Hemisphere conifer and is the tallest extant tree species, reaching heights of over 100 meters (Panshin & de Zeeuw, 1980; Ornduff, 1998). Within the relict population of *M. glyptostroboides*, trees of 50 meters have been reported; essentially the same as the maximum height of 45 meters for *T. distichum* (Elias, 1989; Florin, 1952). *Glyptostrobus pensilis* is a slow-growing short tree that is generally less than 30 meters in height (Dallimore *et al.*, 1967). However detailed ecological and morphological information on *G. pensilis* is lacking and mature trees growing in native populations may exceed 30 m in height.

Based solely on hydraulic considerations, *S. sempervirens* should be the strongest competitor since, in theory, it could overtop the other species. *Metasequoia glyptostroboides* and *T. distichum* should be equally competitive based on hydraulic efficiency. *Taxodium distichum* is the strongest in static bending (i.e., resistance to buckling failure). In *sempervirens* slightly exceeds *distichum* in *specific modulus* (MOE/SG), an attribute that is maximized in trees that are tall or are adapted to dynamic forces such as wind (Jagels *et al.*, 2003; Niklas, 1992). Both *T. distichum* and *S. sempervirens* are mechanically and hydraulically equivalent to or superior to *M. glyptostroboides*. This evidence suggests that hydraulic and biomechanical factors are not competitive limitations for *T. distichum* or *S. sempervirens*. However, the significantly higher wood density of *T. distichum* compared to that of *M. glyptostroboides* suggests that this might be a negative factor when competing in a high latitude environment of low light, and possibly limiting soil nutrients. The greater allocation of resources to stem biomass could reduce crown development and competitiveness for light (Jagels *et al.*, 2003).

4. WATER USE EFFICIENCY

Previously we have shown that the photosynthetic WUE is significantly higher for *M. glyptostroboides* than for several other conifers (*L. laricina*, *Picea rubens* Sargent, *Pinus banksiana* Lambert), particularly at moderately low light intensities (500 μmol $m^{-2}s^{-1}$ or less), similar to those found at high latitudes (Jagels & Day, 2004). These measurements were taken on trees growing under natural diurnal light and summer temperatures at 45°N, Maine, USA.

Figure 11-2. Greenhouse experiment with trees growing under normal diel (DL, on right) or continuous (CL, on left) illumination conditions.

In 2002 we established a replicated (3 block) experiment in a controlled temperature greenhouse with two light regimes, one under the natural diel light (DL) and one under continuous light (CL). Four tree species were randomly mixed in the blocks—*M. glyptostroboides*, *T. distichum*, *S. sempervirens* and *L. laricina* (Figure 11-2).

The CL treated trees were provided with overhead shading designed to: (1) mimic the low intensity light regime of 80°N; and (2) equilibrate light fluence for CL and DL treatments. After approximately three months of growth the trees were measured for leaf level WUE using a LiCOR (LI 6400) open flow system.

The WUE results for the trees growing under DL and CL regimes are illustrated in Figure 11-3. Under DL the three members of the Cupressaceae have significantly higher WUE values than *L. laricina*, and this is most notable at the lower light intensities, which mimic the high latitudes. *Taxodium distichum* and *S. sempervirens* have WUE values as great as or greater than *M. glyptostroboides*. Under CL conditions WUE is reduced somewhat for the Cupressaceae, but is improved for *L. laricina* under the lowest light intensities. At 500 μmol $m^{-2}s^{-1}$, CL, *M. glyptostroboides* and *L. laricina* are essentially equivalent, but *T. distichum* and *S. sempervirens* still have higher WUE values.

The results of this experiment indicate that WUE is not limiting the ability of *T. distichum* or *S. sempervirens* to compete with *M. glyptostroboides* at high latitudes. At the same time it provides evidence that *L. laricina*, unlike any of

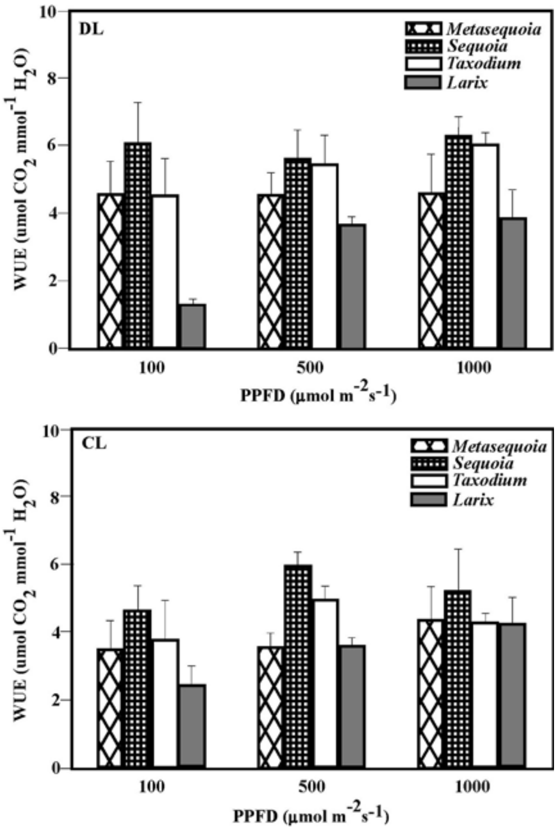

Figure 11-3. Water-use-efficiency (WUE) of 4 tree species exposed to 3 months of normal diel (DL) light (upper graph) or continuous (CL) light (lower graph) at 3 light intensities.

the three Cupressaceae species, has improved WUE under CL compared to DL conditions. At this time we have no mechanistic explanation for this adaptability of *L. laricina*, but if *L. laricina* is a reliable NLR for the fossil *Larix altoborealis* LePage *et* Basinger that grew in the high latitudes, as suggested by Jagels *et al.* (2001), this finding of improved WUE under CL provides supporting evidence for this adaptability.

5. PHOTOBIOLOGY

Previously we demonstrated that *M. glyptostroboides* growing under DL conditions had a photosynthetic light-response curve that showed a steep response to increasing light intensity under low light conditions and reached photosaturation at light intensities of less than 500 µmol $m^{-2}s^{-1}$ (Jagels & Day,

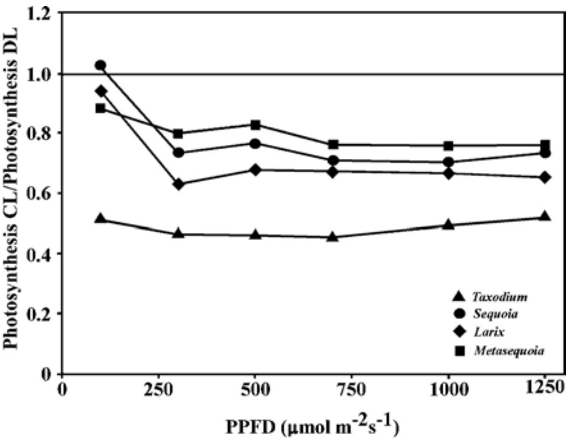

Figure 11-4. CO_2 fixed under CL conditions by *M. glyptostroboides* (Met), *S. sempervirens* (Seq), *L. laricina* (Lar) and *T. distichum* (Tax) as a ratio of that fixed under DL conditions (solid line at 1.0 indicates no change between DL and CL).

2004). Photosynthetic light curves, using the LiCOR system, were developed for *M. glyptostroboides, T. distichum, S. sempervirens* and *L. laricina*. These trees had been growing for three months in either DL or CL conditions.

The photosynthetic rate of plants developed under CL conditions relative to plants developed under DL conditions are compared in Figure 11-4. At all light levels *Taxodium* shows a 50% or greater reduction, while the other three species show only minimal reduction at the lowest light levels, increasing to about a 20% reduction for *M. glyptostroboides* and *S. sempervirens* at 500 µmol $m^{-2}s^{-1}$. *Larix laricina* is intermediate, but closer to *M. glyptostroboides* and *S. sempervirens* than to *T. distichum* (Figure 11-4).

6. DISCUSSION

Based on our experiments we conclude that the best explanation for the rarity of *Taxodium* at the highest paleo-latitudes is linked to limitations in photobiology under CL conditions. *Taxodium distichum* displays the greatest negative divergence in photosynthetic response between DL and CL over the full range of light intensities. Low light levels characterize the arctic spring when competition for light space is greatest for a deciduous tree species (Kozlowski & Pallardy, 1997). *Larix laricina*, a species which photosaturates at higher light intensities than *T. distichum* under DL conditions, adapts significantly better to CL conditions.

A secondary limitation for *Taxodium* could be related to resource allocation. Under the weak light intensities of the high paleo-latitudes, the development of a large efficient crown for light interception would likely have had higher competitive advantages than the allocation of carbohydrates to increase stem xylem density. We view this as a minor secondary factor, however, because *L. laricina* has wood density comparable to *T. distichum*; green basis SG of 0.42 for *T. distichum* and 0.49 for *L. laricina* (Anon, 1999).

Sequoia sempervirens, based on photobiology, WUE, wood density and hydraulic conductance, seems to be ideally adapted to the high-latitude paleohabitat. It equals or surpasses *M. glyptostroboides* in these attributes. Therefore, one can make the case that the evergreen habit of *Sequoia* is the leading candidate as the factor excluding from or limiting the presence of this species in the warm, high Arctic during the Eocene. Read & Francis (1992) grew Southern Hemisphere evergreen trees in complete darkness for 10 weeks at either 4°C or 15°C and compared survival rates with trees grown under natural winter daylength at 1°C. Most of the trees survived, but some tissue death was observed and this was greater in the 15°C dark treatment. We grew *S. sempervirens* in Maine (45°N) during the winter months in a greenhouse with temperatures that averaged about 8°C. The trees survived but had some tissue damage and did not respond well for several weeks after light and temperature were increased. Beerling & Osborne (2002) found a reduction in total, non-structural carbohydrates in the leaves of *S. sempervirens* following a winter light regime that simulated conditions at 69°N. All of these observations suggest that the change from the evergreen to a deciduous habit did not occur under conditions of a warm dark winter, but rather the deciduous habit was a prerequisite for successful colonization of the warm lowlands of the high latitudes.

One puzzling question remains. Since *Sequoia* seems to have been absent from the highest latitudes of North America, but was present as a minor component in Eurasian high latitudes, is this the evidence for speciation suggested by Chaney (1951)? If so, could these now extinct *Sequoia* species have been deciduous? Our data suggests that they probably were not deciduous, or else they would have been more successful competitors with *Metasequoia*.

Since most extant *Larix* species tolerate very cold temperatures, including *L. laricina* which grows to tree line, one might conclude that the fossil *Larix* species found at high latitudes during the Eocene were growing at high altitudes along with *Picea* and *Pinus* species. However, *in situ* stumps of *Larix altoborealis* as well as fertile and vegetative remains have been identified and described from the lowland swamp strata, mixed in very low proportion with *Metasequoia* (LePage & Basinger, 1991; Jagels *et al.*, 2001). In a previous study we suggested that *Larix* likely would have been a poor competitor with *Metasequoia* at the high paleo-latitudes (Jagels & Day, 2004). Its presence at these sites is probably in part due to its ability to survive in acidic, anaerobic bogs. *Metasequoia glyptostroboides* requires the higher oxygen levels found in moving water (Chu & Cooper, 1950; Kuser, 1999). Even today *Larix* is a poor competitor on better sites, but maintains a wide latitudinal distribution by being able to occupy marginal wet sites (Fowler *et al.*, 1995). The evidence we have presented here adds two other features that could favor *Larix* at high latitudes: (1) a photobiology that although it is somewhat less favorable than *M. glyptostroboides* and *S. sempervirens* under CL conditions, is significantly better than *T. distichum*, and (2) an improvement in WUE under CL conditions. *Larix laricina* was the only species that showed improved WUE in CL compared to DL conditions.

Beerling & Osborne (2002) grew several tree species under CL with CO_2 enrichment. They found that photosynthesis was enhanced by more than 40% in *Ginkgo biloba* L. and *M. glyptostroboides*, but *S. sempervirens* and *T. distichum* were not stimulated. This may have provided another competitive advantage to *Metasequoia* in those paleo-environments that were richer in CO_2 (Royer *et al.*, 2001a). However, much of the Tertiary may have had CO_2 levels comparable to the present (Royer *et al.*, 2001b). Therefore, the capacity for enhanced photosynthesis under higher CO_2 levels may have originated at some earlier time period, and has been retained as a vestigial feature up to the present.

7. ACKNOWLEDGEMENTS

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PART IV

Cultivars and Horticulture

Chapter 12

Selecting and Propagating New Cultivars of *Metasequoia*

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Abstract: First a test was performed to compare allozyme variation in a 52 seedlot collection of *Metasequoia* Miki imported from China in 1990, versus that in the 1949 Arnold Arboretum collection. The plants in the greenhouse and in a provenance plantation were examined to identify desirable new cultivars for introduction. Six were selected. To determine the best method to propagate these by cuttings, two hormones and eight different months were compared, using a mist bed. The best times of year appeared to be February/March and August/September. Introduction of three new cultivars is planned: a full, vigorous clone, a narrow clone and a weeping clone.

Key words: China; cloning; cultivar; Hubei Province; Modaoqi; Shui-sha-ba Valley.

1. ORIGINS

In the 1980s, nearly all of the dawn redwoods (*Metasequoia glyptostroboides* Hu *et* Cheng) in the United States were either trees grown from

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the Arnold Arboretum's 1949 seed or trees vegetatively propagated from the originals. Some were already quite large (Kuser, 1982, 1999). The only named cultivar was 'National', a narrow form selected by Frank Santamour at the National Arboretum, Washington, D.C. Also at that time, there was a saying in the trade that all the 1949 seed had come from the single large tree at Modaoqi (Mo-tao-chi), Shui-sha-ba Valley, Hubei Province, China, depicted in Chaney's 1948 booklet "*Redwoods of the Past*". In 1985, we decided to import seed from a rangewide sample of trees, for three reasons:

1) To compare the allozyme variation of the known specimens from the 1949 Arnold Arboretum introduction, with that of the new rangewide sample;
2) To test the truth of the saying that the 1949 seed had come from one big tree. It was thought that this was unlikely, because a study of inbreeding depression in this species (Kuser, 1983) seemed to conflict with a statement of James Clark of Princeton that his share of the 1949 seed "grew like hair on a dog".
3) To screen seedlings of the new seedlots for desirable cultivars.

The New Jersey Forest Service, Arnold Arboretum and several *Metasequoia* enthusiasts raised $5,000 to enable Prof. Li Minghe of Huazhong University, Wuhan, China to collect seeds from 52 parent trees in Hubei (Hupeh), Hunan and Sichwan (Szechwan) provinces (Figure 12-1). These were collected in 1990 and sent to Rutgers late in the year. Because of customs delays, they were received too late that year to sow and were not germinated until February 1991. In that month, seeds of each seedlot were placed on moist filter paper in Petri dishes in a germination cabinet. As soon as each had roots and cotyledons, they were transferred to small pots, then to larger pots, etc. In September 1992, a provenance plantation composed of 352 seedlings and averaging 0.5 m in height was established at the Ryder's Lane Plantation, Rutgers University, New Brunswick, New Jersey. The plantation was laid out in 4 randomized blocks of 60 trees each, with each block containing 3 trees each of the 20 seedlots. The blocks were surrounded by a single row of border trees grown from 27 seedlots, which had not provided enough seedlings to include in the blocks. A duplicate set was shipped to Dawes Arboretum, Newark, Ohio, 100 seedlings were taken to the Arnold Arboretum, 10 seedlings were sent to Morton Arboretum and about a dozen were given to the Morris Arboretum and the Scott Arboretum.

2. CULTIVAR SELECTION

During the summer of 1992, while the seedlings were still in the greenhouse, morphological differences began to be noticeable (Figure 12-2). There were partial albinos, two "corkscrew" variants, a yellow and several progeny of parent tree no. 3 with relatively small, bluish needles (Kuser *et al.*, 1997). These latter

Figure 12-1. Parent tree of *Metasequoia glyptostroboides* from the Shui-sha-ba Valley, Hubei Province, China. Photograph by Li Minghe.

trees varied from upright, fast growing types to semi-weeping dwarfs that grew very slowly. Cuttings of both types were rooted, a dozen of the upright trees were given to Princeton Nurseries, and the dwarf trees to Morris, Bailey and Willowood Arboreta. The original plant of one dwarf (clone 3B), now only 2 m tall (Figure 12-3), is growing at the Morris Arboretum's miniature railroad and the blue uprights are under test at Princeton Nurseries.

Over the next 10 years, the fastest growing, fullest, most vigorous clones in the Rutgers plantation were identified. Cuttings of promising candidates (clones 27A, 34A, 29B and 18A) were rooted and grown side-by-side for one summer in large pots. Clone 27A was tallest in these tests for three consecutive years, and in 1997 a photo of a 1-year-old plant 192 cm tall was published (Kuser *et al.*, 1997; Figure 12-4).

In the summer of 2001, Andrea Bonville of Princeton Nurseries and this author selected a narrow clone (44A) and a wide one (32A) at the Ryder's

Figure 12-2. Clonal variation seen in the 1992 *Metasequoia glyptostroboides* seedlings.

Figure 12-3. Dwarf *Metasequoia glyptostroboides* clone 3B.

Figure 12-4. Metasequoia glyptostroboides clone 27 (large tree on the right) growing at the Ryder's Lane Plantation, Rutgers University, New Jersey.

Lane Plantation for propagation and further testing. Two of the 1949 Arnold Arboretum clones were also selected: 'Clark 3', a 35 m tree in Princeton with as nearly perfect a shape as that seen in *Cryptomeria* 'Yoshino'; and 'Bailey No. 1', Bailey Arboretum, Lattingtown, NY, (near Locust Valley) probably the largest tree outside of China (35 m high and 5.5 m in circumference in March 2002). Cuttings of these trees were grown for comparison with clone 27A. The best clones will be introduced commercially as soon as their propagability, nursery performance and retention of desired characteristics can be assured.

3. PROPAGATION

Metasequoia glyptostroboides can be propagated clonally by grafting or by cuttings. Most clones root easily, or moderately so. The species also grows readily from seed, and even self-sows to some extent, but results in a mixture of types. Clonal propagation is usually done through cuttings because this is low-tech, easy and inexpensive. *Metasequoia glyptostroboides* close relative, *Sequoia sempervirens* (D. Don) Endlicher, can be tissue-cultured and is commercially propagated by axillary bud micropropagation, a variant of this technique. These methods have not been attempted with *M. glyptostroboides* to the best of our knowledge.

The cutting-rooting technique needed to be optimized to multiply selected cultivars efficiently. Rooting of softwood cuttings in August or September had been standard practice at Rutgers, but some nurseries propagated dormant cuttings in the winter. Comparative data were needed for different clones, different

Table 12-1. Comparative Rooting of Five *Metasequoia glyptostroboides* Clones X2 Hormone Levels at Rutgers University, New Brunswick, New Jersey, Spring 2001

Clone	Stuck/Rooted Hormodin 2	Stuck/Rooted Hormodin 3	Total Cuttings Rooted	
			No. Rooted	% Rooted
27A (8 m tree)	7/7	7/6	13	93
32A (8 m tree)	7/5	7/1	6	43
44A (8 m tree)	7/1	7/5	6	43
'Bailey 1' (20 m tree)*	7/1	7/0	1	7
'Clark 3' (35 m tree)	7/0	7/0	0	0
Total by Hormone	**14**	**12**	—	—

*20 m ramet propagated in 1981 from the original 'Bailey 1'.

hormone concentrations and different times of year. To make these comparisons, a mistbed with a 6 sec. mist every 6 min., day and night was used (shutting off the mist at night had been tried, but cuttings dried out). Four-to-five inch (10–12.5 cm) cuttings were inserted into 10 in^3 (166 cc) Leach tubes (98 tubes per 1 ft. × 2 ft. (30 × 60 cm) rack, (Stuewe & Sons, Corvallis, OR) filled with Pro-Mix BX (Premier Horticulture Ltée, Riviere-du-Loup, Québec, Canada). Leaves and side shoots (when present) were removed from the lower 4 cm of each cutting and the basal 1 cm was wounded on one side with a sharp knife. The wounded end was dipped into hormone powder, and inserted into a hole made with a nail after the mix had been moistened. Hormone powder was either Hormodin 2 or 3 (Merck), mixed with Benlate (DuPont) fungicide (19:1) to prevent rot.

In April 2001, clones 27A, 32A, 44A, 'Clark 3' and 'Bailey 1', were compared. Clone 3B dwarf was omitted because it was known to root easily. On 4 April, 7 cuttings of each of the 5 clones × 2 hormone levels were stuck. The clones were judged to have rooted as soon as a white root stuck out of the bottom of the tube. When rooted, they were potted into containers filled with Pro-Mix. The results were recorded on 16 July 2001 (Table 12-1).

All cuttings, which grew after being potted, survived the following winter; those that did not grow failed to break bud the following spring. A hundred and twenty more cuttings of 'Clark 3' were stuck on 1 August 2001 with Hormodin 2, but none rooted.

In March 2002 a time-of-year experiment was begun, using clone 27A (same tree), Hormodin 2 and 7 or 14 cuttings the first week of each month. The cuttings were stuck in March, April, June, July, August, September, October '02 and February and March '03. None were taken in May because of soft growth and wilting, and none in November, December or January. On 25 November 2002, the rack of cells containing the cuttings was moved from the mistbed to a "cold house" (ambient temperature down to 0°C, but no freezing). The cuttings were returned to the mistbed on 1 March 2003, and all live cuttings flushed new

Table 12-2. Rooting of *Metasequoia glyptostroboides* Clone 27A Cuttings at Rutgers University, New Brunswick, New Jersey in 2002 and 2003.

Month	Stuck/Rooted	Percent	First Rooted
March 2002	14/12	86	31 May ‘02
April 2002	7/5	72	24 June ‘02
June 2002	7/3	43	5 August ‘02
July 2002	7/3	43	4 September ‘02
August 2002	7/6	86	13 November ‘02
September 2002	14/13	93	21 March ‘03
October 2002	7/4	57	28 April ‘03
February 2003	14/11	79	26 April ‘03
March 2003	14/13	93	23 May ‘03

growth by 21 March 2003. During these rooting trials, the air temperature in the greenhouse (where this experiment shared space with several others) was usually about 18°C by day and 13°C at night in the cooler months, and 23°C (day) and 18°C (night) in the warmer months. Bottom heat (20°C) was used in February, March, April and October. Results are shown in Table 12-2.

With our efforts to propagate ‘Clark 3’ by cuttings from the big tree frustrated, we turned to two plants of this clone that we had rooted in 2000. These were 2 m tall in March 2003, grew in full sun and appeared vigorous. Cuttings were taken on 10 March 2003, and by 16 June 9 of 14 had rooted and been potted.

On 27 June 2003, the mean height of 10 February 2003 cuttings was 35.4 cm and the mean height of 8 March 2003 cuttings was 27.2 cm.

4. DISCUSSION

The differences in rooting among the clones 27A, 32A and 44A clearly show the clonal variation in this trait. Poor rooting of ‘Clark 3’ was probably due to the size and circumstances of this 35 m tree. That is, the lower branches of which only a few are left are too shaded, while the upper crown is too mature. These difficulties did not exist with the two 2 m open-grown plants—9 of 14 cuttings rooted (64%). The same may be true of ‘Bailey 1’. A trial of cuttings from a 2 m plant of this clone vs. a 2 m plant of 27A is planned for spring 2004.

The greater height of February 2003 cuttings (vs. March 2003) indicates that for growers who want larger plants earlier, February is the best month to stick cuttings.

5. SUMMARY

1) There are clonal and tree-size differences in the rootability of *M. glyptostroboides* (see Kuser, 1987).
2) Hormodin 2 and 3 work equally well.
3) Hardwood cuttings stuck in February or March root as well as softwood cuttings stuck in August or September.
4) Difficult trees/clones such as ‘Clark 3’ need special treatments such as juvenilization, grafting or budding.
5) The naming and introduction of several selected *M. glyptostroboides* clones are planned for 2004.

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Chapter 13

Cultivars of *Metasequoia glyptostroboides*

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Abstract: A comprehensive list of cultivars of *Metasequoia glyptostroboides* Hu *et* Cheng is provided together with a brief description of the features that make each cultivar distinct from the type specimen. Included is a list of putative varieties and species that require further study.

Key words: color; cultivar; horticulture; hybrid; Netherlands; varieties.

1. INTRODUCTION

Numerous cultivated varieties (i.e., cultivars) of *Metasequoia glyptostroboides* Hu *et* Cheng have been identified since its discovery over a half century ago. The botanical variety differs from the cultivated variety, which is not a nomenclatural taxon, but simply a variant or hybrid that possesses some economic or aesthetic value. The cultivar is often used in horticulture, landscaping or urban forestry because of the uniformity they display in characters such as foliage color, branch angle or overall growth form. The phenotypic

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uniformity of cultivars results from asexual propagation practiced by commercial nurseries (e.g., rooted cuttings, grafting or other cloning methods). Because cultivars are maintained by human cultivation they normally would not occur widely without man's influence. The following is a list of horticultural variants of *M. glyptostroboides*. Some of these varieties are commercially propagated whereas others are limited to much smaller scale propagation.

2. *METASEQUOIA GLYPTOSTROBOIDES* VARIETIES

'Bonsai' (Kuser *et al.*, 1997; J. Kuser, personal communication, 2001): This tree is a dwarf weeping cultivar with some bluish-green leaves. This tree grew approximately 50 cm in height and 65 cm in width over 4 years. John Kuser of Rutgers University and A. Bonville of Rutgers University selected this variant among the seedlings that were planted at the Ryder's Lane Plantation at Rutgers University in 1992. The seedlots were obtained from 47 new parent trees from Hubei, Hunan and Sichuan Provinces, China. The original tree is growing at the Morris Arboretum, Philadelphia, Pennsylvania.

'Emerald Feathers' (Callen, 1976; Dirr, 1998): A vigorous clone with dense brilliant green feathery foliage. This tree is growing at the Hillier Arboretum, England.

'Golden Dawn': A cultivar discovered by Kenneth W. Murray. A natural mutant from seeds of the species, sown in 1986. The original tree is cultivated in Wilmington, Del., USA. 1,5 m high in ten years with 1,2 m spread.
The main characteristics are its globose shape, slow growing and golden yellow leaves. Needs partial shade the afternoon. This cultivated variety is mentioned in the US Patent & Trademark Office Website.

'Gold Rush' (Royal Horticultural Society Plant Finder [RHSPF], 2004): This recent cultivar comes from Japan and possesses yellow foliage. It is recognized under different names such as 'Golden Oji', 'Golden Mantle' and 'Ogon'. It roots well, but dry soil conditions sometimes cause the leaves to burn. This tree was introduced in Europe by P. Zwijnenburg Nurseries, Boskoop, The Netherlands in 1993 and commercialized in 1997-1998. Its growth was 6 m over 10 years. It comes from irradiated seedlot by X-ray (in 1974). The original tree was planted in 1977 at the Kameyama breeding station, Institute for forest Tree Improvement, New Oji paper co., Ltd, Mie, Japan. This cultivar is mentioned in the US Patent & Trademark Office Website.

'Green Mantle' (RHSPF, 2004): There is no description for this tree that is referenced in the Royal Horticultural Society plant finder. The name was proposed by J. Fryer Nurseries in Hull, England and accepted by the Royal Horticultural Society.

'IFG': This is an upright variant. This horticultural variety is mentioned in the Stanley & Sons Nurseries (Oregon) catalog.

'Jack Frost' (T. Buchholz, personal communication, 2002): This tree was found in 1989 in a group of 2 year-old seedlings and introduced by Bucholtz & Bucholtz, Oregon, USA. It roots easily from summer or winter cuttings. The tree appears to be slower growing and more compact than typical *M. glyptostroboides*. Although vigorous when young, the original tree is was only 15 feet tall and 9 feet wide after 15 years of age. A creamy-white frost is present on the upper surfaces of the leaves and is most noticeable from above because the variegation can be lost in the sky when looking up at an older tree.

'Matthaei Broom': Found in 1989 as a witch's broom at the Matthaei Botanical Garden, USA. It grows approximately 8 to 15 cm per year and 90 cm to 180 cm after 10 years. It is mentioned in the American Conifer Society database.

'Miss Grace' (T. Buchholz, personal communication, 2002): This tree is a slow-growing weeping form with small needles. It was previously known as 'Semi-prostrata W.B.', which is an invalid name. Its growth is not vigorous and supposedly obtained with material from a witch's broom. It was recently introduced by Buchholz & Buchholz Nursery, Oregon, USA and should be compared to 'Bonsaï'.

'Moerheim' (Wyman, 1970): This cultivar possesses branches that are more or less upright and is columnar in its habit. It also was one of the seedlings grown from the original 1948 seedlot that was sent abroad by the Arnold Arboretum. The parent tree is thought to be growing at the Belmonte Arboretum in Wageningen, The Netherlands.

'National' (DeVos, 1963; Wyman, 1970; Callen, 1976; Dirr, 1998; RHSPF, 2004): This was the first cultivar named by Frank Santamour of the United States National Arboretum, Washington, D.C. This seedling was discovered from the original seedlot that was distributed by the Arnold Arboretum in 1948. It is known for its narrow pyramidal shape.

'Nitschke Cream' (Dirr, 1998): It is a tree with new cream-colored growth that becomes green with maturity. The trunk, peeling, has an attractive black color. It is thought to be scorched in full sun.

'Prof Ching' (J. Kuser, personal communication, 2001): Tree with a spreading form and wide branching angle and similar to that seen in *Taxodium distichum* 'Monarch of Illinois'. John Kuser and A. Bonville selected this variant in 2000 from the seedlings planted at Rutgers University in 1992 and named in honor of Professor Ching, who was John Kuser's major professor. The seedlots were obtained from 47 new parent trees from Hubei, Hunan and Sichuan.

'Prof Li' (J. Kuser, personal communication, 2001): A narrow and compact tree. John Kuser and A. Bonville selected this variant in 2000 from the seedlings planted at the Ryder's Lane Plantation, Rutgers University in 1992 and named in honor of Professor Li Minghe who sent the seedlots to John Kuser from China. The seedlots were obtained from 47 new parent trees from Hubei, Hunan and Sichuan.

'Rowena' (Dirr, 1998): This tree possesses leaves with white edges. The variegation is not chimeral, but it appears to be a genetically controlled mutation where the plastids turn from green to white or white to green during the annual growth cycle.

'Rutgers Select' (J. Kuser, personal communication, 2001): A vigorous clone that grows up to 2 m per year. John Kuser and A. Bonville selected this variant in 2000 from the seedlings planted at Rutgers University in 1992. The seedlots were obtained from 47 new parent trees from Hubei, Hunan and Sichuan Provinces, China.

'Sheridan Spire' (Dirr, 1998; RHSPF, 2004): This tree was discovered in 1968 and introduced by Sheridan Nurseries, Canada. The tree is narrower than 'National' and 20 m tall trees range from 3 to 5 m in width.

'Shui San' (J. Kuser, personal communication, 2001): Pyramidal tree that is as symmetrical as *Cryptomeria* 'Yoshino'. The spacing of the branches is much closer than that seen in *M. glyptostroboides*. John Kuser and A. Bonville selected this variant in 2000. It is one of the trees grown by James Clark of Princeton University from an Arnold arboretum 1949 seedlot. It is planted at Broadmead, Princeton, New Jersey, USA and was 35 m high in 2000.

'Spring Cream' (RHSPF, 2004): This vigorous tree possesses new leaves that are yellow-cream in color and take on a pale green hue during the summer. This variant is thought to have been introduced by Wiel Linssen, The Netherlands, who is a specialist in dwarf conifers. Its size is similar to the type and is different from 'Nitschke Cream'.

'Vada' (Wyman, 1970): This variant is another tree growing at the Belmonte Arboretum and was named in 1967 by Broekhuizen and Zwart of the Institute of Forestry Research in Wageningen. 'Vada' possesses horizontal branches and is densely pyramidal. It was grown from the original 1948 seedlot that was sent to Europe by the Arnold Arboretum.

'White Spot' (RHSPF, 2004): This tree possesses irregular variegation and the leaves are sometimes completely white and very small. It was found growing in a garden in The Netherlands sometime in the early 1980s and introduced by P. Zwijnenburg Nurseries in 1997–1998.

'Waasland': This tree possesses an interesting erect form with a trunk and branches that are dark brown to black. The deciduous branchlets are erect too. This variant was discovered in the late 1970s and named by Mr. Decalut, Director of the Waasland Arboretum, Belgium. It was selected from seeds imported from China.

3. PUTATIVE CULTIVARS

The following varieties are often considered as synonyms of *M. glyptostroboides*. Further study may permit erection of cultivar status for some.

- *Metasequoia glyptostroboides* Hu *et* Cheng *var. caespitosa* Y.H. Long & Y. Wu: This form is characterized by possessing large cones.
- *Metasequoia honshuenensis* Silba *et* Callahan: This taxon possesses large cones that are up to 35 mm in diameter and thick peduncles that are up to 85 mm long. The leaves are 20–43 mm in length. The new stems are blue in color. This is a fast growing cultivated tree.
- *Metasequoia neopangaea* Silba: This tree is cultivated and differs mainly from others in that it possesses oblong-cylindrical, hexagonal or polyhedral cones with about 30 scales.
- *Metasequoia glyptostroboides* 'Crackerjack': This is a small compact erect tree that has been proposed for cultivar status by Jardin Jasmin, Québec, Canada. It is approximately 1/3 of the width of *M. glyptostroboides*.
- *Metasequoia glyptostroboides* 'Little Giant': A small erect tree with chocolate brown bark and grows approximately 20 to 25 cm per year. This potential variety has been proposed by Conard-Pyle Co. USA and is not yet available.
- Nelis Kools of Kools Nursery, Deurne, Netherlands has selected approximately 20 seedlings among 15000 seedlings over the last several years (N. Kools, personal communication, 2003). These seedlings include several forms such as dwarf, golden, variegated or with very small needles. Some trees will be selected and named in the next years.

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Chapter 14

A CONSERVATION PLAN FOR *METASEQUOIA* IN CHINA

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Abstract: Models for resource protection are examined in this chapter, including the program challenges and successes for the redwood forests in California, rainforests in Central and South America, coral reefs in Australia and the giant panda in China. A *Metasequoia* Conservation Plan is discussed and tools for assessing effectiveness of conservation programs are suggested. In addition, the Appendices include an education plan, a *Metasequoia* fact sheet, funding sources, international support organizations and an example of an endangered species management plan.

Key words: California redwoods; conservation assessment; dawn redwood conservation; *Metasequoia glyptostroboides,* redwood conservation; resource protection models; *Sequoia sempervirens, Sequoiadendron giganteum.*

1. INTRODUCTION

At best, the protection of an endangered species is a challenging endeavor that becomes even more formidable in nations such as China where the intense pressures of rapid population growth must be confronted. Protection of the dawn redwood, *Metasequoia glyptostroboides* Hu *et* Cheng will require setting aside land that is needed now or in the future for agricultural production. Industrial pollution further damages *M. glyptostroboides* forests, and ecological changes resulting from the Three Gorges Dam project could cause future impacts. Thus, a conservation plan for the protection of *M. glyptostroboides* in China must take into account the scarcity of remaining native trees, the demand for agricultural land conversion, the isolation of potential forest groves and environmental stressors that are likely to continue. The plan should focus on habitat preservation, and the planning process must include a broad array of stakeholders, including scientists, governmental policy makers, non-governmental organizations (NGO's) and local citizen representatives. Funding will be needed from local, regional and central government agencies, paired with assistance from the NGOs and the general public.

2. HISTORY OF *METASEQUOIA GLYPTOSTROBOIDES*

Metasequoia Miki was discovered in 1941 by Shigeru Miki (Miki, 1941), while examining Pliocene fossils of redwoods and swamp cypresses, *Metasequoia glyptostroboides* was determined to be a new tree species based on its fossil record, and named to be "akin to the Sequoias." In 1943, Zhan Wang collected samples of a tree in Moudao, called by locals, Shui-Shan or Water Fir, and W.C. Cheng verified that the tree was a "living fossil" of *Metasequoia* (Ma, 2003). The documentation and description of these living trees previously known to science only as fossils was a lengthy and collaborative effort, involving researchers both inside and outside China (Chaney, 1948; Hu, 1948; Merrill, 1948). A recent chronology, prepared by Jinshuang Ma, details events of this ongoing saga, after review of an extensive literature in Chinese and English, and examination of original herbarium specimens (Ma, 2003).

The well-documented fossil record of *Metasequoia* indicates that the species had achieved a wide distribution early in its evolutionary history (LePage & Yang, 2002; LePage *et al.*, this volume), and demonstrates the continuity of its morphological and paleogeographic changes over the past 100 million years (Ma) (Yang & Jin, 2000). Molecular genetic information will likely provide insight into the conditions of its restricted living populations, possibly yielding critical information for the management and conservation of living populations of *M. glyptostroboides* (Yang, this volume). For example, the ancient Paomu tree in Hunan Province has been shown to preserve unique micromorphological characters of the leaf cuticle and thus contributes to the overall genetic diversity of the species (Leng *et al.*, 2001; Leng, this volume; Yang, this volume).

As an example of present-day populations of this "living fossil," a naturally occurring grove of *M. glyptostroboides*, located in Hubei Province in southwest China is thought to number about 5,400 trees. This "collective woodland" managed by the local government, comprising about 6000 ha^2 is located in the Xiaohe Valley, Lichuan County, Hubei Province, at about 600-1500 m elevation (Liu & Wang, 2002). The *M. glyptostroboides* populations are scattered among 25 villages near Lichuan, and are distributed in the hills and wetlands; most of the populations are small (average density $= 8$ trees/km^2), usually comprised of less than 30 trees/population (Cheng *et al.*, 2002). A few remaining trees are located in Hunan Province (Yang, personal communication).

The *Metasequoia* has been nominated as a possibility to be selected as China's national tree (China Internet Information Network [CIIN], 2003a). However, subtle threats exist, probably due to a lack of knowledge about the significance of the *M. glyptostroboides*. For example, when the Shanghai Agriculture and Forest Bureau announced plans to spend six million yuan (US $722,892) for rebuilding two national parks, they stressed that all the trees in Dongping Forest were comprised of *M. glyptostroboides*, which made the forest "boring to look at" and "easy for disease and insects to spread." The Bureau's spokesman noted that the replanting in Dongping Park would consist of 40 species of trees, purchased from seedling nurseries nearby, and expressed hope that changes in the forests would help attract more tourists (CIIN, 2003b). In addition, climate change, expanding human development, food production, and infrastructure changes such as large hydroelectric projects may also impact the future viability of *M. glyptostroboides* groves.

Representing one of China's national treasures, the native *M. glyptostroboides* populations are in dire need of an endangered species preservation plan. This chapter provides an analysis of the challenges of developing and implementing an effective conservation plan for native *M. glyptostroboides* in Hubei Province, and sets forth policy guidelines and offers suggestions for initiating the planning process. A discussion of possible funding mechanisms is also included.

3. GENERAL GUIDELINES FOR RESOURCE PROTECTION

Resource protection efforts elsewhere may provide models for managing *M. glyptostroboides* forests. Effective public policies should generally meet the following criteria: (1) Provide realistic solutions; (2) Be feasible and cost-effective; (3) Achieve broad-based acceptance by stakeholders; and (4) Provide good long-term and short-term success. These criteria could be used for evaluating different conservation tools discussed later in this chapter (Table 14-1).

Effective conservation programs usually encompass public and private support and funding, and must begin with an overall vision or master plan. Although the funding necessary to set aside large tracts of land or preserve an endangered resource may take time to accumulate, a visionary plan accompanied by modular implementation can make such projects feasible. The most successful projects also have strong champions who passionately believe in the importance of their ventures. To build the broad-based support of stakeholder groups, successful projects must also utilize effective marketing techniques including compelling imagery and memorable phrases (e.g., the campaigns to save whales, Giant Panda, Great Barrier Reef and rainforests). Although most people can relate well to saving endangered species; the process of raising sufficient awareness of a particular endangered species is more challenging. Yet, there is general agreement that the continued existence of humans as a species depends on the careful maintenance of other species, from the tiniest microbes to the tallest trees. "If we cannot maintain a balance between our needs and the

Table 14-1. Evaluating the effectiveness of conservation policy initiatives*

CRITERIA	1	2	3	4	5	Score
A. Solves Problem						
B. Feasible Implementation						
C. Cost Effective						
D. Accepted by Stakeholders						
(1) Political Decision-Makers						
(2) Government Oversight Agencies						
(3) Scientists						
(4) Local Citizen Representatives						
(5) NGOs						
E. Short Term Success Achievable						
F. Long Term Success Possible						
TOTAL SCORE						

*Effectiveness rating technique developed by G.A. Langlois in conjunction with an Environmental Policy course at Bryant University. Criteria are rated from "most effective" (score = 5) to "least effective" (score = 1).

needs of other organisms, the earth will eventually cease to sustain life as we know it." (Davies, 2001, p. 256).

The Ecological Society of America (ESA) suggests that "the primary cause of global biodiversity losses has been widespread human transformation of once highly diverse natural ecosystems into poorly managed ecosystems." (ESA, 2002). Thus, by improving species management techniques it may be possible to mitigate some of the damage already done. The World Resources Institute (WRI), an organization dedicated to improving the use of the Earth's natural resources, has developed a program for working with developing countries to establish plans for preserving natural resources and maintaining global sustainability. One WRI effort focuses on working with national governments to encourage the use of more efficient agricultural processes that can meet human needs without accelerating the rate of species decline (WRI, 2003). These tools might be especially valuable in China, where impending agricultural expansion seems to be in direct conflict with preservation efforts.

4. SPECIFIC CHALLENGES OF PRESERVING *METASEQUOIA GLYPTOSTROBOIDES* FORESTS

Given the scarcity and isolation of the remaining *M. glyptostroboides* forests and the realities of land use conflicts and pollution threats, it is essential to set forth a long-term plan for habitat preservation, as quickly as possible. However, preservationists are faced with formidable challenges, including, but not limited to, the following tasks:

- Identifying potential sites for preservation, mostly located in isolated, rural settings;
- Working with local residents and government agencies to develop feasible and effective programs;
- Incorporating scientific knowledge into the design of protection efforts;
- Creating a compelling commitment to implement a long-term plan;
- Developing an convincing marketing effort;
- Funding the preservation effort; and
- Acting in time to save a sufficient number of groves (biological sustainability).

Each of these challenges requires different areas of expertise; yet, the multiple elements of such a preservation plan must be tightly integrated, with sequential phases carefully aligned with funding and governmental support.

The overall low genetic diversity of *M. glyptostroboides* poses a serious threat to the survival of its native populations (Yang, this volume). Although *M. glyptostroboides* is cultivated worldwide, as isolated individuals or clusters, low genetic diversity exists among cultivated trees; therefore, new plantations should be encouraged to utilize multiple genetic-distanced sub-populations, and unique individuals such as the Paomu tree in the Hunan Province should be protected (Yang, this volume). Population genetics data for 46 *Metasequoia* seedlots showed an average to low genetic diversity, accompanied by inbreeding (Kuser *et al.,* 1997), and recent studies of trees from the same region have revealed that considerable genetic isolation has occurred (Li & Yang, 2003). Thus, it will be important to foster genetic diversity in any preservation program for *M. glyptostroboides*, and to integrate an effective research component into the conservation plan.

There is strong phylogenetic alignment of *M. glyptostroboides* with *Sequoiadendron giganteum* (Lindley) J. Buchholz (Giant redwood) and *Sequoia sempervirens* (D. Don) Endlicher (Coast redwood). Thus, we will examine some of the threats facing the North American redwoods and review some of the successful preservation efforts. There are many lessons to be learned from successful preservation efforts and a brief review of a few examples might reveal how these lessons could be integrated into a *M. glyptostroboides* preservation plan.

5. PRESERVATION OF THE CALIFORNIA REDWOOD FORESTS

*Sequoiadendron gigan*teum and *S. sempervirens* are endemic to California, and millions of years ago their range extended across North America, as far north as Alaska and British Columbia (Baker, 1965). Today, *S. gigan*teum is limited to a narrow strip on the western slopes of the Sierra Nevada Mountains and confined to 75 groves (Baker, 1965). About one third of these groves lie within the *Sequoia* and King's Canyon National Parks, but half (38) are in the adjoining *Sequoia* National Forest. Other groves are scattered throughout state lands, federally managed land, a Native American Reservation and on private land. *Sequoia sempervirens* is located along the western slope and valleys of the coastal mountains, ranging from the southern edge of Oregon to the Big Sur area south of Monterey, California. These two species, along with *M. glyptostroboides*, have been described as representing "the endpoints of three long lines of separate evolution" (Baker, 1965). *Metasequoia glyptostroboides* exhibits a deciduous behavior, although closely associated with evergreen species (Baker, 1965; Yang, this volume).

Early chromosomal analysis indicated that *M. glyptostroboides* is more closely related to *Sequoiadendron* J. Buchholz than to *Sequoia* Endlicher (Stebbins, 1948), but later chromosomal studies suggested that the two California redwoods are more closely related to each other than to *Metasequoia* (Schlarbaum *et al.*, 1983). However, there is a "general affinity among *Metasequoia*, *Sequoia* and *Sequoiadendron* as a natural clade within the family Taxodiaceae" (Yang, this volume). Immunological analysis of proteins confirmed the grouping of *Metasequoia* with the two American redwood species (Price & Lowenstein, 1989), and more recent DNA sequencing data further substantiated these findings (Yang, this volume). Further studies suggest a possible Jurassic divergence time for the origin of the Sequoideae (Li & Yang, 2003).

Sequoiadendron giganteum is found along a 420 km belt extending from Placer County, near the America River, south to Tulare County, along the Deer River. The habitat is at an elevation of 1,372 m, on the western slopes of the Sierra Nevada Mountains. The rainfall in this area ranges from 420 to 1520 mm yr^{-1}, which falls mostly as snow (Baker, 1965). Excessive dryness and extreme cold limit the species, and the trees are seriously damaged by prolonged cold stress. *Sequoiadendron giganteum* have the greatest bulk of any tree in the world, e.g., "General Sherman" in *Sequoia* National Park is 9.1 m in diameter at chest height, with an estimated volume of 1,486 m^3. The trees commonly exceed 90 m in height, and many exceed 300 years in age. The oldest "authenticated" age of a downed tree is 3,200 years (Baker, 1965). *Sequoiadendron giganteum* are found in groves, or stands of related trees, on western slopes of the mountains. The naturalist, John Muir, noted "that groves are found on unglaciated slopes separated by glaciated valleys" (Baker, 1965). In the northern locales, the valleys are too cold in winter for this species. Similarly, living specimens of *Metasequoia* show an increased sensitivity to freezing under high carbon dioxide concentrations (Royer *et al.*, 2002).

Sequoia sempervirens is among the world's tallest trees, with many individuals exceeding 91 m in height, with the tallest known tree 112 m in 1956 (Fritz, 1957; Fowells, 1965). The tallest trees are 400-800 years old. The largest trees are around 6 m in diameter at chest height. *Sequoia sempervirens* thrives in the climate of northern California, where fog is an important source of moisture in the summer months, and the trees require a minimum of 1020 mm of annual rainfall (Baker, 1965). Severe frosts, hot winds and low rainfall limit sequoia sempervirens; hence, the summer fogs are essential, and the period of time between the cessation of the winter rains and the summer fogs is crucial to their survival. The Coast redwoods growing on alluvial flats store large volumes of water in their trunks (one 76 m tree held roughly 30,280 l of water); this stored water helps to alleviate evaporative stress during summer months (Stone, 1965). Mean annual temperatures in coastal redwood habitats vary from 10° to 16°C with a frost-free period of 6-11 months (Fowells, 1965). *Sequoia sempervirens* produce abundant seed almost every year, with seed viability increasing with the age of the parent tree (Fowells, 1965). Vegetative reproduction occurs commonly, with sprouting from stumps or roots of a tree (Baker, 1965), at any time of the year within 2 or 3 weeks after logging (Fowells, 1965). Wildlife in the coastal redwood forests includes several rare or unusual species, including the Bald eagle, Northern spotted owl, American peregrine falcon, Marbled murrelet (CERES, 2004) and a number of amphibians including ocelot-spotted giant salamanders, tailed frogs and seep salamanders (Bakker, 1972, Waldron, 1998; USGS, 2004).

Sequoia sempervirens is fire resistant, with bark up to 41 cm thick, and old growth redwood stands show evidence of three or more severe fires each century (Fowells, 1965). The trees are brittle and shatter when they fall; the pieces were collected by woodsmen and salvaged for “shingles” for houses (Redwoods, 2002). The weather resistance of the wood has made it a popular choice for homeowners, with uses ranging from fences, decks, outdoor furniture, shingles, roofing, etc. (Brinegar, 2002); and led to a tremendous economic pressure for harvesting the redwood forests.

The *S. sempervirens* forests were known to native Americans more than 10,000 years ago, and early colonists recorded finding the redwood in Monterey County (Snyder, 1992). Thadeys Haenke, botanist of a Spanish expedition in 1791 collected herbarium specimens and redwood seeds, probably in the Santa Cruz area. There is at least one tree still growing in Spain as a result of his efforts (Snyder, 1992). However, the taxonomy of the *S. sempervirens* remained elusive for many decades. A German botanist, Steven Endlicher, in 1847 named the Coastal redwood *S. sempervirens* (Snyder, 1992; Chaney, 1951).

The redwood forests are fire-prone ecosystems, but the trees are fire resistant and usually respond quickly following a fire. Drought causes severe damage, because the trees have shallow root systems. However, the trees also have the capacity to store water. The southern range of *S. sempervirens* is limited by the time period between the winter rains and the summer fogs. High temperature and low rainfall heighten wind damage in the summer. Human activities, including enhanced fire potential and seemingly endless logging projects, further threaten the forests.

The native *M. glyptostroboides* populations in China share many features with the California redwoods, including similar habitat (high rainfall, moderate altitude, low to moderate genetic diversity and extensive habitat fragmentation). In both cases, land use conflicts make preservation efforts more difficult. However, the California redwoods face additional pressures, such as damage from recurrent fires and harvesting by the timber industry.

6. PRESERVATION ISSUES IN CALIFORNIA

The economic resource value (value of a "cut" tree) of redwood forests is high because of the excellent quality of the wood, its high retail value and the high productivity of the forests, including the high output of lumber from a tree, combined with the rapid growth of new trees. By comparison, the bioresource value of the trees (value of a living tree) must also be considered, including the importance of maintaining biodiversity throughout the world, including endangered species like the redwoods. An argument could be made that some species are "destined" for extinction because they are no longer well matched to their surroundings, including factors such as climate change and widespread fires, but the counter argument might suggest that it is primarily human interference that threatens the redwoods, so therefore we must try to help. Another quandary we face in "managing" to protect the "big, old trees" is whether the groves will eventually reach senescence and die out. Given the low to moderate genetic diversity, this could also be an issue for isolated *M. glyptostroboides* forests.

Many challenges confront regional decision makers charged with effectively managing these unique bioresources. Conflicting value systems often translate into confusing policies regarding the preservation or use of a given resource. In the case of the California redwood forests, there has probably always been a general respect for the age, size and grandeur of the trees and a tendency to preserve at least remnants of the once-extensive redwood forests. However, the high economic value of redwood lumber has resulted in a premium price in the marketplace and engendered an attitude of "cut now, worry later" encouraging the timber industry to harvest the trees at an accelerating pace. For example, on river flats, up to a million board feet per acre have been recorded (Snyder, 1992).

For decades, the United States has struggled to balance the preservation of these ancient giants with the intrinsic economic value of this resource. Preservation programs have included efforts by national, regional and local governments, often by setting aside parklands, and by a variety of conservation organizations and citizen activists. The remaining redwood forests in California, representing only a small fraction of the original old growth ecosystems, support many threatened and endangered wildlife species, including the California condor. Historically, *S. sempervirens* grew in California condor country. In fact, the last condor captured in the wild was found nesting in a *S. sempervirens* tree (Natural Resources Defense Council [NRDC], 2002). Additionally, many rare species of plants and animals thrive in the old growth forests, including the California spotted owl, wolverines, Pacific fisher, mountain lion, American marten, yellow-legged frog and northern goshawk (NRDC, 2002).

In spite of these uncertainties, several protection programs have been developed, and a few trends seem to have emerged: (1) A general shift from a reliance on national efforts alone (lands set aside, laws regulating logging practices or protecting endangered species) to a greater dependence on partnerships involving state programs and private initiatives; (2) Within the public sector, protection programs have shifted emphasis from preserving single target species, to "ecosystem management" and protection (i.e., protection of old growth forests in an effort to preserve working environments and therefore confer a greater chance of survival); and (3) A shift away from seeing redwoods only as a source of lumber to its recognition as a threatened species worthy of protection.

In general, as long as the public perception prevailed that the forests remained plentiful, there were fewer objections to the timbering activities. When awareness caught up with the realities of the shrinking forests, there was outcry from the general public to preserve what forests remained. However, when an entire region's economy is tied to a particular industrial sector, such as timber harvesting, cessation of that activity is likely to cause severe economic impact. Not only is there a measurable reduction in actual job opportunities, there is also an identity crisis experienced by the rugged outdoorsmen who have played crucial roles in the timber industry. Often these workers have been woodcutters for generations, and they cannot imagine any other kind of job. Consider the economic realities facing a worker who knows that every tree he cuts down is worth a lot of money to his family, while, if left standing, the tree will merely be a tourist attraction. The timber companies, who stand to lose considerable profits if the forests were to be designated off limits for harvesting mature trees, focus on this anguish facing workers. Given that many of these multinational companies value long-term forest management less than short-term profits, the situation becomes even more intense. Consequently, the preservation programs often result in severe conflict among the various stakeholders.

In addition to stakeholder conflicts, there may also be disagreements between local residents who are tied to the economic resource value of the forests and regional or national interests who favor resource protection. Biologists describe the value of preserving worldwide biodiversity, especially unique organisms, rare and endangered species or keystone species within a given habitat. Ecologists may argue for better ecosystem management, emphasizing the importance of the redwood forests as unique habitats and therefore a heritage to be protected for all the peoples of the world. Others may emphasize the importance of preserving the remaining redwood forests for future generations. Yet, most of these defenders of the redwoods will not be asked to underwrite the costs of preservation through lost jobs or economic strain. So, a second dynamic emerges, wherein local needs do not necessarily match regional or national priorities.

Other conflicts may involve ownership of the land, whether public or private, and power struggles may unfold around which agency or organization is entitled to make the decisions about preservation versus harvesting the economic value. In his book, *Should Trees Have Standing*, Christopher Stone argues that someone must be empowered to speak in court for the rights of creatures without a voice, especially when destructive actions are pending (Stone, 1996). Thus, an essential question arises as to whether endangered trees have the "right" to be defended against their early demise, and if so, whose responsibility is it to raise the defense.

7. PRESERVATION STRATEGIES FOR CALIFORNIA REDWOODS

The following tools have been used for preserving the California redwoods: National parks and federal protection programs; federal laws protecting endangered species; state parks and protection programs; local government or quasi-governmental agencies such as watershed associations; and private organizations (Schrepfer, 1983; Noss, 2000). Each of these approaches offers advantages and brings liabilities and often partnerships for bringing together a variety of protective tools. Examples of these programs are listed in Table 14-2. The summary is not intended to be exhaustive, but rather, illustrative of the diversity of programs currently involved in the preservation of redwoods.

Several conservation organizations have shown a consistent commitment to preserving the remaining redwood forests, including non-profit public charities, the Sempervirens Fund, dedicated to preserving coastal redwoods, and the Save the Redwoods League (SRL), set up by the Garden Club of America (GCA) for the purpose of protecting redwoods (Yaryan *et al.*, 2000; GCA, 2002; SRL, 2002). Gifts from private citizens, for example, the estate of Russell Varian, and Senator Jesse and Louisa Metcalf, have also played crucial roles in

Table 14-2. Summary of Redwood protection sites in California

Name	Location	Size (Acres)	Date	Sponsor/manager	Funding	Species protected
Giant Sequoia National Park	Near Three Rivers, CA (Rt.198)	385,000	1890	National Park Service (NPS)	Federal Funding, Estate Gift of Russell Varian	Giant Sequoia
King's Canyon National Park Grant Grove	Near King's River	462,000	1940	NPS	Federal Funding	Giant Sequoia
Yosemite National Park	East of San Francisco	748,000	1890	NPS	Federal Funding	Giant Sequoia
Humboldt Redwoods State Park	"Redwoods to the Sea Corridor"	52,000	1918	State of California	Save the Redwoods League (SRL); State of California	Coast Redwood
Headwaters	Near Eureka	7,000	1999	U.S. Bureau of Land Management	Federal Funding State of California	Coast Redwood
Redwood National Park	North of San Francisco	60,000	1968	NPS	Federal Funds	Coast Redwood
Castle Rock State Park	Santa Cruz Mountains	3,513	1959 1968 1999 2000	State of California	Estate Gift of Russell Varian; Sempervirens Fund	Coast Redwood
Jedediah Smith Redwoods State Park*	Smith River, near Crescent City, CA	10,000	1929	State of California; NPS		Coast Redwood
San Lorenzo River Redwoods	Santa Clara Valley	1,340	2001	State of California (linked to Castle Rock)	Sempervirens Fund Varian Family Foundation	Coast Redwood
Mill CreekPreserve	Del Norte Coounty	25,000	2002	SRL; State of California (Dept. of Parks & Recreation)	SRL State of California U.S. Fish & Wildlife Service	Coast Redwood
Jesse & Louise Metcalf Grove	Near Jedediah Smith State Park	960	1942	SRL	Garden Club of America	Coast Redwood
Big Basin State Park	Santa Cruz Mountains	18,000	1902	State of California; NPS		Coast Redwood
Del Norte Coast Redwood State Park	Near Crescent City, CA	6,400	1929	State of California, NPS		Coast Redwood
Prairie Creek	Del Norte Coast	14,000	1920's	State of California; NPS	SRL; Garden Club of America, State of California	Coast Redwood
Garden Club of America Grove	Canoe Creek (Eel River) Humboldt County	5,131	1931 1972 1974	State of California	Garden Club of America Save the Redwoods League State of California	Coast Redwood

*Jedediah Smith was an early California explorer (1826).

setting aside protected groves (Sempervirens Fund, 2002a; P. Sharpe, personal communication, 2002).

Personal actions were sometimes undertaken to dramatize the plight of the endangered redwoods, for example, the "tree sit-in" of Julia Butterfly Hill, who took up semi-permanent residence in a large 1,000-year old coastal redwood, in a fight with Pacific Lumber Company, in order to prevent the tree from being cut down (Hill, 2000). Since her courageous stand, others have volunteered in different regions of the California coast, to save a particular individual tree, or grove of trees, often forcing a resolution between conflicting economic and ecological values in a particular region.

Public/private partnerships are of special interest in the California experience. For example, the GCA Grove was first established in 1931, when members raised $91,634, and gave the money to the Save the Redwoods League, for purchase of 2,552 acres in the Canoe Creek watershed, along the south fork of the Eel River in Humboldt, California. In 1972, more land was purchased, and in 1974, the final acquisition was made, bringing the Grove to 5,130.72 acres. SRL and the State of California have spent $3 million to complete the grove, which now represents the first complete ecological unit of forest and watersheds in the California State Park System. This is now the third largest protected redwood grove in California (GCA, 2002; SRL, 2002).

A summary of the primary protection programs for the California redwoods is presented in Table 14-2. This summary serves to illustrate the wide variety of programs, the relative size of the areas under protection, and the types of funding mechanisms that have been utilized.

Another example of public/private partnerships for protecting redwoods is the purchase of 1,340 acres of redwood forests by the Sempervirens Fund from the San Lorenzo Valley Water District, in the area of Santa Clara, at a price of $3.4 million ($10,000/acre). A new summit trail will allow hikers to view Monterey Bay, and the protected reserve will be eventually added to Castle Rock State Park (Sempervirens Fund, 2002b). Another dramatic purchase of an ancient redwood grove (Headwaters) located just south of Eureka, California, from Pacific Lumber Company, required the efforts of two governors, a U.S. senator, and a state senator, and carried a price tag of $480 million of federal and state monies, with a $130 million state contribution (San Francisco Chronicle, 1999). The Headwaters deal provided Pacific Lumber long term stability without the prospect of lawsuits and regulatory fights, while the logging restrictions on remaining land held by the Company satisfies the protection needs of environmental advocates. Redwood groves will be off limits for logging, and streams containing Coho salmon will require buffer zones (San Francisco Chronicle, 1999).

The creation of the Mill Creek Preserve was predicated on negotiations by the SRL, and was funded collaboratively by the SRL, the State of California and the U.S. Fish and Wildlife Service (Office of the Governor, 2002). A unique feature of this project was the joint purchase of a $5 million annuity by the SRL and the Stimson Lumber Company of Portland, Oregon (former owner of the land), to provide in-lieu-of-tax payments to Del Norte County for the next 20 years (Office of the Governor, 2002).

In summary, we have learned many valuable lessons from the saga of the destruction and protection of the California redwoods.

- We should not wait to undertake preservation efforts until the resource has dwindled below sustainable levels.
- We must protect resource areas before full-blown economic development occurs because of the infrastructure demands of cities (water, sewage treatment, drainage outfalls, transportation systems, residential needs, commercial facilities and waste disposal sites) result in clearing of the land, contamination of the watershed and reduction in air quality. Furthermore, the land values rise dramatically, making it more difficult for public and private entities to purchase land for public open space and habitat protection.
- Good solutions involve many stakeholders (including lawmakers and the general public).
- By envisioning protection programs within a system approach, environmental and economic planners, resource scientists, biologists and preservationists can better work together. Viable solutions must take into account timbering practices, lumber markets, land use patterns and ecosystem management.
- Economic benefits to private users (i.e., timber companies) must be tied to sustainable business practices (e.g., saving old forests, using selective harvesting techniques and carefully evaluating the uses of the wood).
- Forest preservation plans must include scientific research.
- Education programs are an essential component of preservation plans.
- Such programs will work best if the general public has been enlisted at all stages of the process, so that they ultimately “take ownership” of the preservation effort. Involvement of the public-at-large usually results in a more solid commitment to the preservation effort, and connecting with global interests can add another layer of support.

In short, the following formula might well describe the successes of California preservationists thus far:

REDWOODS + SCIENTISTS + PUBLIC PARTICIPANT +
EFECTIVE LAND USE + REGIONAL PLANNING
+ GOOD BUSINESS PRACTICES
=
SUCCESS FOR REDWOOD PRESERVATION

8. ESSENTIALS OF A *METASEQUOIA* CONSERVATION PLAN

It is clear from this brief review of the California experience that we must not delay in addressing the protection of native populations of *M. glyptostroboides* in China, and that a long-term, well designed conservation plan must be created as soon as possible. The Conservation Plan should be designed carefully, so as to address the challenges identified earlier in this chapter, and would typically include the elements listed in Table 14-3 (adapted from the U.S. Endangered Species Act guidelines for Conservation Plans).

Each of these elements will be explored further, to ascertain what strategic actions are needed, to identify other successful conservation efforts that might

Table 14-3. Elements of a *Metasequoia glyptostroboides* conservation plan

Element	Action needed	Time frame
1	Identify potential protection sites	Year 1
2	Create a management scheme for project oversight (address scientific goals, stewardship issues, economic impacts, maintenance plan, habitat complexities, etc.)	Year 1
3	Develop a convincing proposal for *Metasequoia glyptostroboides* protection (to be presented to governmental authorities and funding sources)	Year 1
4	Develop a communication network (*Metasequoia* directory, needs assessment, International *Metasequoia* Association)	
5	Create partnership arrangements with local residents and government agencies to set aside protected areas and to develop stewardship programs	Year 2
6	Design an education program for children and adults, that will foster long-term attitudes oriented toward conservation and protection of *Metasequoia glyptostroboides*, as a symbol of China's natural heritage	Year 2
7	Develop a scientific research plan to complement the conservation efforts (include field and laboratory research)	Year 2
8	Set up Permit Program for scientists to study the protected zones	Year 2
9	Expand and update the *Metasequoia glyptostroboides* field research station	Year 1 & 2
10	Develop an effective marketing plan (gain public support and obtain funding)	Year 2
11	Determine the phasing of the Conservation Plan's implementation	Year 2
12	Create a non-profit entity that will procure funding and oversee implementation of the Conservation Plan	Year 2
13	Raise funds to support the Conservation Plan	Year 1 & 2
14	Develop assessment tools for determining the success of implementation for each phase of the Conservation Plan	Year 2

provide techniques or guidelines, and suggest possible resources that could enhance the success of implementation.

8.1. Site Identification

Identification of a site that would be a good candidate for protection will not be an easy task. First, most of the areas where the native *M. glyptostroboides* populations are likely to be found are located in remote and isolated regions, usually with limited access. Locating an ideal site will require the cooperation of scientists, regional and local authorities, local residents and will necessitate using aerial surveys, field identification and geographical information system (GIS) techniques. Since the entire Conservation Plan will be phased over several years, it would probably be desirable to focus on the identification of one site as an initial effort, to be viewed as a pilot project for initial implementation of the Plan.

This initial site should be relatively small, well contained, have a high probability of sustainability and represent a valuable research area. By meeting these criteria, a greater chance of success could be realized. Furthermore, procuring funds for setting up the protected area would be easier if the initial project represents a modest effort. An initial site might be targeted at about 200 km^2 – 600 km^2. Going forward, other protected preserves could be identified. Other criteria for selecting the appropriate conservation site would include the localized economic impact (to reduce disturbance of local lifestyles, and provide possible opportunities for limited ecotourism). Additionally, an assessment team should evaluate the present versus the future value of the protected forest. A team of scientists and governmental authorities should begin work immediately on site identification.

8.2. Management Scheme for Project Oversight

An organizing team should be assembled to develop a management scheme for implementing the *Metasequoia* Conservation Plan as quickly as possible. This team should comprise individuals representing many classes of stakeholders (scientists, forestry managers, conservationists, governmental agency staff, local community leaders and specialized NGOs). Issues that need to be addressed will include the following: local economic impacts; stewardship issues; the cultural setting; scientific research goals; long-term maintenance requirements; initial funding mechanisms; access and use limitations; and sustainable forestry practices. One of the decisions to be made is whether the Conservation Plan will include plans for limited ecotourism, or if it will be more desirable to reduce human impacts as much as possible. The management scheme will probably include a Board of Advisors, or some similar oversight committee to deal with specific strategies and ongoing decisions.

8.3. Formal Proposal for *Metasequoia* Protection

To move forward toward implementing the *Metasequoia* Conservation Plan in China, it will be helpful to draft a formal proposal that can be submitted to government officials, scientific organizations, funding sources and other interested parties. Although the format for this proposal might not be as detailed as the Conservation Plan, it must include compelling arguments for the protection of native populations of *M. glyptostroboides*. Other crucial elements include a brief description of the potential site for preservation, summary of the management scheme, education plan, and marketing approach and potential funding sources. This summary could be structured in a manner similar to a statement of intent for a grant proposal. In addition, it would be valuable to create a simple brochure to highlight the main points of the proposal, and to include photographic images of the target area. These materials should be drafted as soon as possible.

8.4. Communication Network for *Metasequoia* Conservation

An international communication network needs to be set up to allow for improved sharing of information on *M. glyptostroboides* research, field observations, distribution patterns, climatic limitations, protection efforts and funding sources for preservation. Although informal channels of information currently exist, complementing scientific journals, a more structured approach would facilitate the implementation of an effective *Metasequoia* Conservation Plan.

The first step is to create a *Metasequoia* Directory, including all researchers, forestry managers, government agencies and NGOs whose scope of interest includes protection of endangered tree species such as *M. glyptostroboides*. The Directory should be assembled immediately, and should include an Internet version.

Second, the International *Metasequoia* Association should be formed, on the model of other small, specialized scientific societies. Since the purpose of this society will be bring together scientists, field managers and other parties interested in all aspects of *Metasequoia* study, the membership should then be inclusive, rather than exclusive. Because many members may have limited funds, the membership fees should be modest. It is envisioned that a separate non-profit foundation will be established to procure funding for the implementation of the *Metasequoia* Conservation Plan (see Section 8.12); this will allow the International *Metasequoia* Association to focus on sharing information, planning for international conferences and fostering of scholarly endeavors for the protection of the *M. glyptostroboides*. Both of these entities should take responsibility for raising awareness of the plight of the native *M. glyptostroboides* populations to the various international agencies and NGOs that are focused on forest protection and forest program coordination (see Appendix E for a short list of some of these organizations).

A quarterly or bi-yearly newsletter should be distributed to all interested parties and shareholders, including updates on the development and implementation of the *Metasequoia* Conservation Plan, funding, public outreach, and scientific findings. Each issue of the newsletter could focus on a local volunteer or student initiative. An Internet version should also be posted, in both English and Chinese (and other languages as necessary).

The last step of the communication process is to seek information from all interested parties on a Needs Assessment for protecting *M. glyptostroboides*. This step can be initiated under the jurisdiction of the International *Metasequoia* Association, but future updates will be incorporated into the overall Management Scheme that is built into the Conservation Plan (see Section 8.2).

8.5. Partnership Collaboratives for Setting Up the Protected Reserve

The *Metasequoia* Conservation Plan should include a set of Partnership Collaboratives that are designed at a very early phase of the Conservation Plan. These collaboratives should be set up among appropriate governmental agency personnel, local villagers and community leaders and local scientists and foresters. The purpose of forming these collaboratives is to create a forum for discussion of local impacts, changes of lifestyle, opportunity costs, ownership of the protected forests, long-term maintenance and stewardship, required limitations on access or use and the possible local benefits of cooperative arrangements. These collaboratives will also set the stage for the implementation of local education programs and possible replanting or reseeding programs. The experience gained through the collaboratives will provide an additional tool for having local citizens and government agencies take “ownership” of, and develop a sense of identity with the protected *M. glyptostroboides* forests. If future eco-tourism sites are developed, local villagers could be trained as “ecoguides” (LePage, personal communication; Geatz, 2002). Villagers would also be excellent sources for natural history observations and local lore regarding *M. glyptostroboides* trees. The data acquired could then be used further in marketing the preservation of the forests.

8.6. Education Program to Accompany the *Metasequoia* Conservation Plan

An Education Program will be needed, targeted toward children and adults. The education modules should be designed to inform learners about the importance of preserving the *M. glyptostroboides* (as an endangered species) and the significance of its ancient history (a part of China's natural heritage). The Education Program should include both curriculum modules and teacher training modules. The educational component of the Conservation Plan will serve to foster long-term attitudes toward conservation and protection of *M. glyptostroboides*. In addition to local programs for schools near the protected reserves, an effort should be made to have the curriculum modules adopted throughout China, as well as internationally. An Internet site should be set up with a version available to Chinese teachers. In addition, field programs could be developed for hands-on learning; this could become a component in the ongoing monitoring programs within the protected reserve, or in conjunction with the field station.

Initial actions should include an assessment of existing education programs in China and then a survey of similar models elsewhere, e.g., in conjunction with the California redwood protection programs. A sample outline for an Education Program is included in Appendix B of this chapter.

8.7. Scientific Research Plan

To identify the appropriate site for a protective reserve and to design a management plan for overseeing the project, it will be necessary for scientists studying *M. glyptostroboides* to set forth appropriate goals for research, field monitoring and site management. Additionally, the scientists will need to suggest the level of protection needed for the forest, design an appropriate mapping program, monitor the extent of genetic variability, assess growth parameters, develop a program for dealing with potential insect infestations, determine whether the protected reserve is a significant sample of a native *M. glyptostroboides* forest and evaluate the sustainability of the site. Additionally, questions regarding whether it is desirable and/or possible to reconstruct the ancient forest environment to support the growth of *M. glyptostroboides* need to be addressed. Meanwhile, studies of *M. glyptostroboides* and its fossils can serve as a template for better understanding ancient forests.

Existing knowledge/information at the current research station needs to be available to visiting scientists, and future data needs to be available to the research stations. Scientists will also need to help in structuring an appropriate stewardship program.

8.8. Permit Program for Scientists and Bioresource Specialists

A permit program for tracking scientific research within the *M. glyptostroboides* protected preserves may be necessary, in order to protect the interests of all stakeholders. This process can add a layer of protection that no damage will occur to the protected trees due to research protocols, or from living accommodations (camping, etc.), or that no untoward impacts will occur for local villagers. In addition, all research efforts should take into account the stewardship arrangements that have been set up. Australia has set up an effective permit system for researchers on the Great Barrier Reef, and this might be a useful model (see discussion of the Great Barrier Reef protection programs). The permit program should be straightforward and easy to administer and if possible be Internet-based, so that visiting scientists can easily provide the needed information and receive a timely response prior to their arrival in China.

8.9. Expand and Update the *Metasequoia* Field Research Station

The activities of the current *Metasequoia* Field Research Station need to be expanded and their staff, equipment and funding requirements should be assessed. Founded in 1973, the Lichuan Dawn Redwood Management Station has surveyed the native *M. glyptostroboides* stands three times between 1972 and 1984. These data have been supplemented by investigations of scientists from the College of Life Science at China Normal University from 1986-2002 (Cheng *et al.*, 2002; Liu & Wang, 2002). These databases will be invaluable to future researchers and the findings need to be made widely available in a usable fashion. Funding needs for the station will be addressed in the discussion of Section 8.13 (see below).

8.10. Effective Marketing Program for *Metasequoia* Conservation

Metasequoia glyptostroboides needs to be marketed as a Chinese national treasure, and as important cultural icon. Additionally, and particularly important for funding procurement, is the fact that the *M. glyptostroboides* is an intrinsic part of China's natural heritage, thus important to all citizens in the nation. The tree is often described as a "living fossil" because it was first identified from fossil samples, and then later found alive. These images can be used to persuade governmental officials and funding sources of the value of preserving *M. glyptostroboides*. The existence of accessible fossil sites helps to document the ancient history of the species, and will be particularly convincing.

The marketing strategy will be targeted at several distinct markets, each of which will necessitate special attention to the marketing package, the content and the presentation:

- Local villagers, local community leaders, and local governments;
- Provincial and national government officials;
- Chinese national environmental NGOs and forestry organizations;
- Asian nations in the Pacific region;
- International community (United Nations agencies and NGOs);
- Scientific researchers; and
- Funding sources (granting agencies, NGOs, corporations, private donors).

A good marketing plan comprises the "5 P's", and the actions described below could be incorporated into the marketing effort:

Positioning

- Build recognition and awareness of the seriousness of the situation.
- Value of *M. glyptostroboides* to the region and to the world.

Packaging/Promotion

- Create brochures, factsheets, newsletters, web site, multimedia presentations, seminars, etc.
- Use case studies on deforestation and reforestation and conservation of native *M. glyptostroboides* populations.
- Develop programs for distribution of seeds and seedlings.
- Create an "Adopt-a-Tree" program.
- Work with nurseries worldwide to foster conservation of native populations of *M. glyptostroboides.*

Persuasion

- Develop a passion for the protection of *M. glyptostroboides.*
- Use all marketing tools as effectively as possible.
- Encourage all stakeholders to collaborate on conservation goals.

Performance

- Implement and track progress of all marketing initiatives.
- Constantly assess the integration of the marketing plan with other conservation goals.

An important marketing challenge involves garnering the support of Chinese forestry researchers and managers. Potential arguments might include the following factors:

- China's large commitment to and funding for preserving and expanding the country's forests;
- The need for protection of native populations of an endangered species;

- Natural environments for *M. glyptostroboides* thickets often qualify as wetlands, which might be able to be designated as Ramsar Convention wetlands; and
- Added value of carbon sequestration by forests (an actual commodity that can be traded in the world markets of carbon dioxide credits).

For example, researchers have calculated forest carbon storage in China from 1949-1995, and concluded that their results "provide evidence to support the proposal addressed by the Kyoto Protocol that carbon sequestered by afforestation or reforestation could partly offset CO2 emissions from fossil fuel consumption" (Fang *et al*., 2001).

Also, when seeking support from private donors, the marketing emphasis can include the tax advantages of donating to the effort. These advantages are different in Canada and the United States, but are particularly beneficial for estate gifts.

One possible approach to capture the attention of the general public worldwide is to consider the value of making seeds available. The growth requirements of the M. glyptostroboides and whether seeds could be broadly distributed may complicate this effort. However, seed programs have been used effectively for other threatened or endangered tree species. Since the trees are available commercially at some nurseries in the United States, it might be possible to link the protection of native forests to the sale of the cultivated trees. For example, a tag could be attached to the tree inviting customers to donate to the "*Metasequoia* Conservation Fund" or perhaps the growers would agree to contribute a small donation for each tree sold. These are possible ideas that could be explored.

Some immediate actions would include preparation of media brochure and multimedia presentations, particularly for funding agencies, media outlets, and government officials (as discussed earlier under Section 8.3 of the Conservation Plan).

8.11. Phasing of Implementation of *Metasequoia* Conservation Plan

Given the formidable challenges of setting up protected preserves for *M. glyptostroboides* it will be important to act quickly, but to insure a high likelihood of success for the projects. The protection projects should be set up in "phases", in order to learn from our own experience as we move forward. Although there may be overall goals for the Conservation Plan, the first phase should be treated as a Pilot Project, to allow for setting up the management structure, obtaining funding, identifying the initial site to be protected and working out the scientific research plan. Each phase should be treated as a separate entity, with its own funding, and a thorough assessment of its effectiveness. A time line should be developed for the phasing, as soon as the management scheme is set up and the needs assessment is completed.

8.12. Non-Profit Organization (NGO) for *Metasequoia* Conservation

To create an ongoing funding program, it will be necessary to create a foundation with Section 501C-3 non-profit status, and an endowment that will generate sufficient funds to maintain the protected preserves and provide ongoing support. This foundation will be able to receive grants from other NGOs and government agencies, gifts from private donors and qualify for challenge grants. The foundation should be separate from the International *Metasequoia* Association, so that it can be certified as a non-profit entity for tax purposes. The foundation should be set up as soon as possible, once the overall goals for the *Metasequoia* Conservation Plan are established.

8.13. Funding for the *Metasequoia* Conservation Plan

Sources of funding the *Metasequoia* Conservation Plan need to be identified as quickly as possible. Some possibilities will include the following:

- Special gifts from members of the International *Metasequoia* Association (a check-off box on the membership form);
- United Nations Agencies and International NGOs;
- U.S. non-profit organizations (e.g., Nature Conservancy);
- Estate gifts from interested supporters;
- Research fee structure;
- Sale of *M. glyptostroboides* seedlings;
- Sale of *M. glyptostroboides* memorabilia, books, notecards and photos;
- Adopt-a-Tree Program (e.g., 500 trees at $1000/tree would generate $500,000); and/or
- International Corporate Donors.

For example, the Toyota Company has embarked on a $1.2 million tree-planting program in China and provides funds for wide-ranging environmental activities worldwide (Toyota, 2002). Also, the Japanese firm, Oji Paper Company, through their Overseas Forest Plantation Project," has initiated several tree-planting projects in China, and is offering training for forestry management in China (Oji Paper, 2004).

Some initial possibilities for support are listed in Appendix C. A special committee to expand the search for initial funding sources should be set up immediately, with the understanding that the *Metasequoia* foundation will later

Table 14-4. Funding goals for *Metasequoia* conservation plan

Budget item	2002 Budget	Year 1	Year 2	Ultimate goal
Field Station (Director & Operating Expenses)	$4000/yr	$5,000/yr	$6,000/yr	$10,000/yr
Setup Expenses (Foundation & Association)		$500		
Endowment & Grants for Research		$3,000	$20,000	$500,000
Protected Reserves		$25,000	$20,000	$40,000

assume this responsibility. A first step in funding would be the update of the field station (see Table 14-4).

8.14. Assessment Tools for Evaluating the Conservation Plan

A variety of assessments will need to be made in order to ascertain the success of the various components of the *Metasequoia* Conservation Plan, and assessment tools should be selected at the time the management scheme is set up. For example, it will be necessary to assemble a variety of scientific assessments of the protected reserve (growth parameters, genetic diversity, use management, extent of research, mapping, etc.). Also, analysis of funding sources should be completed to evaluate the efficacy of different fundraising techniques (e.g., level of complexity, ease of procuring the funds, short-term versus long-term funding and amount of paperwork involved). The needs assessment updates will help to determine when to phase out existing activities, or phase in new initiatives. The scientific goals will need to be updated periodically, as new information raises additional questions to be pursued. An assessment of the overall Conservation Plan could be done using the Guidelines for Conservation Programs (see Table 14-1).

9. OTHER SUCCESSFUL CONSERVATION PROGRAMS—WHAT LESSONS CAN BE LEARNED?

In addition to the case of California redwood conservation efforts, other initiatives that might provide guiding principles for the development of a *Metasequoia* conservation plan could include the following: attempts to slow down the destruction of tropical rainforests, protection of biodiversity in China and Southeast Asia, development of a conservation plan for The Great Barrier Reef in Australia and restoration of Giant Panda habitat in China. Each of these efforts will be briefly discussed, noting the lessons that can be learned and identifying guiding principles that might be applicable for preserving *M. glyptostroboides* forests in China.

9.1. Lessons Learned from Efforts to Preserve Rainforests

Rainforest destruction and degradation is widespread, encompassing tropical rainforest in Central and South America, Africa, and Southeast Asia and temperate rainforests in the United States and Canada. Tropical rain forests cover 7 percent of the Earth's surface, but account for about 40 percent of the Earth's species (Raven, 2001, p. 376). In 1999, the United Nations Food and Agriculture Organization (UNFAO) issued a report on the "*State of the World's Forests—1999*". The evaluation included 117 countries and noted an annual loss of 0.7 percent per year of the world's forests from 1990–1995. In Southeast Asia, a 1.6 percent loss per year was reported, representing 12.6 million hectares (31.1 million acres) of lost forest. At this rate, these forests will be gone by the 22nd century (UNFAO, 1999; Raven, 2001, p. 410). Others note that about 2.4 acres/sec, 149 acres/min or 78 million acres/year of tropical rainforests are being cleared or severely degraded each year (Rainforest Action Network [RAN], 2004). The extent of destruction varies in each locale, for example, about 8.4% per year of rainforest loss in Thailand, 14.3%/year in Nigeria and 15.6% per year in Cote d'Ivoire, according to 1989 statistics (RAN, 2004). Causes include human settlement, subsistence agriculture, plantations and ranches, timber activities, oil and mineral explorations, charcoal manufacture for industry, hydroelectric dams, building of logging roads, climate change, government subsidies to industry, ranchers, timber companies and settlers (Miller, 1998, p. 360; Raven, 2001; Middle East News Online, 2002; RAN, 2004; Rainforest Information Centre [RIN], 2004; UNFAO, 2003). Subsistence agriculture may account for as much as 60% of the annual losses worldwide, with an estimated 200–600 million people dependent on subsistence farming (Raven, 2001, p. 411). Subsistence farmers are also described as "agriculture-shifted cultivators" to emphasize the likelihood that they are often the landless poor who are forced into the forests in order to survive (RIN, 2004).

Damages resulting from rainforest destruction and degradation includes species loss, habitat loss for migratory birds, localized climate change, reduced carbon uptake and sequestration, soil demineralization, lost "bioprospecting" possibilities (e.g., useful medicines or new food products), loss of reserve species for future "adaptive radiation", erosion and sedimentation of nearby waterways, lost eco-tourism and sustainable agriculture opportunities, and cultural dislocation of tribal peoples (Raven, 2001; RAN; Miller, 1998; UNFAO,

2003. Each forest ecosystem that is lost reduces the complexity and dynamic vitality of the region.

In spite of deforestation losses worldwide, some regions have developed programs to preserve their remaining forest resources, with notable examples from Brazil, Costa Rica, Australia and Asia. For example, in 1999, Brazil agreed to set aside ten percent of Amazonian rainforest for conservation, in a program financed and supported by The World Bank and The World Wildlife Fund (Raven, 2001, p. 410) and the U.S., in conjunction with The Nature Conservancy, has initiated for a "debt for nature swap" in Belize, the Maya Mountain Marine Corridor (Lazaroff, 2004). Recent protection programs are being set up in Africa, partially due to the emphasis placed on this continent by the UNFAO in their most recent report on the world's forests (UNFAO, 2003; Strieker, 1999). Often these protective programs have emerged as a result of worldwide pressure to preserve rainforests, and have included the following techniques: protected reserves; sustainable agriculture and industry; development of ecotourism; strip shelterbelt harvesting; extractive reserves; national and regional parks; and business-to-business enterprises (Starbucks, 2004). A few of these techniques will be discussed in more detail.

Although Costa Rica has lost most of its forest resources, it still has about 25 percent of forest and woodland cover, including lowland rainforests, dry tropical forests and montane forests; however, this represents only about 1.7 percent of the forests that had been in place in the early 1960's, mostly cleared for agriculture (Miller, 1998, p. 352). Costa Rica has an ambitious conservation program, with an extensive network of protected areas with more than 25 percent of the country's land area protected as forest reserves, national parks, teak plantations, and reservations for indigenous peoples (UNFAO, 2003; Miller, 1998, p. 352; Mongabay Project, 2004). The Organization of Tropical Studies (a consortium of 44 U.S. and Costa Rican universities), has been formed to promote research and education in tropical ecology and the National Biodiversity Institute (INBio), a private, non-profit organization, has been set up to survey and catalog Costa Rican biodiversity (Miller, 1998, p. 352–354). The Guanacoste National Park is a small, seasonal forest is being restored and reconnected to the rainforest on an adjacent mountain slope, under the jurisdiction of Daniel Janzen, a Professor of Biology at the University of Pennsylvania; the project involves 40,000 residents, utilizes farmers and residents in replanting programs, and trains students from primary school to college in forest ecology and sustainable forestry management (Miller, 1998, p. 354; Janzen, 2003).

The Monteverde Cloud Rainforest Reserve, administered by the Tropic Science Center, is a private, non-profit reserve that straddles the Continental Divide at 1,440 m (4,662 ft), where more than 100 species of mammals, 400 species of birds, including 30 kinds of hummingbirds, tens of thousands of insect species, and 2,500 species of plants, with 420 kinds of orchids. (Monteverde Costa Rica

Rainforest, 2004). The Santa Elena Cloud Forest Reserve is another private, non-profit reserve, one of the first community managed rainforest reserves in Costa Rica, administered by Santa Elena High School, and dedicated to nature conservation, ecotourism, and the upgrading of local education (Monteverde Costa Rica Rainforest, 2004).

Costa Rica launched a program in 1998 to protect another 500,000 hectares (1.25 million acres) of rainforest by selling greenhouse gas allowances, estimated to eventually remove as much as one million metric tons of carbon dioxide (Mongabay Project, 2004). Other rainforest protection efforts in Costa Rica involve expansion of ecotourism, introduction of a program for private landowners to develop their own sustainable forest management plans, and extensive biodiversity protection programs (Mongabay Project, 2004; Costarican National Chamber of Commerce, 2004). The Rincon Rainforest project in Costa Rica has raised over $2 million from schoolchildren, individual donations, and foundations (Janzen, 2003).

The extent of rainforest coverage in Asia is large; however, rapid population growth in this region, coupled with an insufficient legal structure for protecting natural capital, has resulted in severe habitat loss in some regions (UNFAO, 2003). The Nature Conservancy, a non-profit environmental organization in the United States, dedicated to preserving important ecosystems and "saving the last great places," in 1999 began an important biodiversity initiative in China's Hunan Province, called the "Great Rivers Project" (Geatz, 1999). The project focused on the protection of biodiversity in Hunan Province, and emphasized the importance of involving multiple perspectives in the planning process, working together with local and regional officials, and developing an ecoregional plan. Low-impact ecotourism efforts were included in the planning. Project planners concluded that "cultural preservation is a key concern in the Great Rivers Project," and the government hopes that related tourism will generate jobs and income for Hunan Province (Geatz, 1999, p. 14). In the five years since its inception, some of the initiatives of the Great Rivers Project have included a biogas project to reduce dependency on fuel-wood harvesting, a new school designed as an alternative energy demonstration site (with conservation as part of the curriculum), a low-impact tourism plan and local workshops to train villagers as ecoguides (Geatz, 2002).

Other tools for protecting tropical rainforests include "strip shelterbelt harvesting" by native peoples, currently being done in Peru (Miller, 1998, p. 351); "extractive reserves" that are set aside for indigenous harvesting of natural rainforest products, established in Brazil in 1998 (Miller 1998, p. 355); and business to business arrangements, such as the Fair Trade Certified Coffee program, whereby farmers are encouraged to participate in cooperatives and to sell their beans directly to importers, or the Conservation Coffee program, encouraging shade-grown coffee (Starbucks, 2004). However, the extractive reserve programs are often difficult to sustain, given the tremendous pressure from local developers and international firms to access the rainforest regions for timbering, mining, and ranching. Often little of the profit from the sale of rainforest products filters back to the indigenous harvesters; for example, of the $20 million of imports of Brazil nuts to the United States, only three percent of the New York City price goes back to the nut gatherers (Miller, 1998, p. 355).

Clearly, the forests of the world are endangered by human activity. Overall, we need a detailed and updated summary of the Earth's forests, deforestation and the extent of degradation, using remote sensing tools, and matched to ground level evaluations. The World Commission on Forests and Sustainable Development (WCFSD) recommended in its 1999 Summary Report that we must "accelerate research and training so sustainable forest management can become a reality quickly." (WCFSD, 1999). In its 2003 State of the World's Forests report, the UNFAO described the following needs for forest research: substantial work on carbon budgets; forest research in developing countries; indigenous technology and local technical knowledge; and the use of remote sensing techniques to study forests (UNFAO, 2003).

However, extensive reforestation efforts have been implemented. The UNFAO and The World Bank have cooperated on a project for reforestation in South Korea, using the approach of "community forestry." Villagers have been reforesting the country at the rate off 40,000 hectares (98,840 acres) per year (Botkin, 1995, p. 270). The South Korean government also committed $6 million for reforestation projects in China from 2002–2007 (Xinhua News Agency, 2001). In China, 700,000 farmers have co-operated to plant a green wall to protect crops, by creating a shelter belt of trees 100 m wide, and 4,480 km long (Botkin, 1995, p. 270; BBC Monitoring, 2001). The Great Green Wall of China, started in 1978, is envisioned to eventually cover 9 million acre, stretching from Beijing through Inner Mongolia (Ratliff, 2003).

Planting projects are most successful where local residents, especially women (often a major force for environmental improvement in developing countries) have participated in the planning and implementation. Programs work best that give village farmers incentives (e.g., ownership of the land). Governments of China, Nepal, Senegal and South Korea have established successful tree-planting programs, typically in joint ventures between government agencies and locally elected village forestry associations; typically, in successful reforestation programs, the government supplies villagers with seeds or seedlings and advises them technically on the planting and care of the trees (Miller, p. 356). A 10-year reforestation program in China, covering 97% of the country, and encompassing 76 million hectares (293,436 square miles) of forest, will be implemented, as one component in a 6-part program for reforestation in the country (CIIN, 2003c). Another initiative of interest is a proposed project for planting trees and grasses along the Great Wall of China, to create a vegetative green belt and better protect this World Heritage Site (People's Daily Online, 2000).

Several international forest partnerships have been formed, for the purposes of combating deforestation and degradation and for conserving and protecting unique types of forests. The United Nations Forum on Forests (UNFF) was established in 2000, and charged with carrying out the recommendations of the Intergovernmental Panel of Forests (IPF) and the Intergovernmental Forum on Forests (IFF), with developing a legal framework for all types of forests, with providing financial and technological support for implementing sustainable forest management. In 2001, the Collaborative Partnership on Forests was launched, to support the work of the UNFF, and to act as a catalyst for national, regional, and international action, particularly protection of unique types of forests. These agencies work with the Convention on Biological Diversity (CBD) and their Program of Work on Forest Biological Diversity, to initiate "urgent action to safeguard forests that are threatened, and/or that can contribute to conservation, sustainable use and benefit sharing" (UNFAO, 2003). Other international forest organizations are listed in Appendix E. As we move forward with the *Metasequoia* Conservation Plan, it will be necessary to forge relationships with the appropriate United Nations agencies and with other international forest organizations, as sources of information and possible financial support.

In summary, some of the lessons learned from rainforest protection programs in various parts of the world would include the following:

- Effective conservation programs are more difficult for developing countries with high debt, rapid population growth and a history of resource extraction.
- We need a detailed and updated summary of the Earth's forests, deforestation and the extent of degradation, using remote sensing tools and matched to ground level evaluations.
- Corruption in local and regional government can be countered by global attention to the destruction of tropic rainforests.
- Protecting forests requires setting aside sufficient land so as to achieve large, functioning ecosystems that can be bequeathed to future generations.
- Effective programs require international partners (funding sources, market development, technical assessments, etc.).
- Direct business to business enterprises can create local markets for forest products, leading to sustainable forestry practices.
- Eco-tourism can be too successful, with resulting damage to the ecosystems under protection, and increased pollution associated with the tourist infrastructure.
- The timber industry needs to change their harvesting practices, relying more heavily on selective cutting and long-term ecosystem management; government officials need to enforce laws and guidelines that protect rainforests.

- Planners and policy makers must work with scientists to conduct ecological assessments of each forest resource, in order to identify the areas most worthy of conservation, and to establish effective management plans.
- Reforestation and forest protection programs work best if they are community-based and involve villagers in planning, implementation and follow-on activities.
- International funding agencies must evaluate not only the degradation potential of a proposed development project, but also consider whether proposed conservation and mitigation plans are sound.
- Education programs are an essential component of effective preservation plans. Young people are the managers of the future.
- Independent international assessments of major conservation efforts are important, because local and national officials are under tremendous economic, social, and political pressures to cut conservation funding, bypass restrictions, subsidize powerful agricultural and industrial entities and ignore corrupt practices.
- Economic losses associated with wasted resources, government subsidies, and lost opportunities for ecotourism and sustainable forest management must be calculated and used to compare to the costs of setting aside and managing conservation areas.

9.2. Lessons Learned from Australian Efforts to Preserve the Great Barrier Reef

The Great Barrier Reef (GBF), stretching along the East Coast of Australia for approximately 1,430 miles, is composed of over 2,900 reefs, 890 fringing reefs, 300 coral cays and over 600 continental islands, and is home to approximately 500 species of seaweed, 4,000 species of mollusks, 400 species of coral, 1,500 species of fish, 20 species of sea snakes, 6 breeding species of turtles and over 200 species of birds (Pivotal Ecosystems International, 2004). The GBF is thought to comprise 8 percent of the world's fish species, and to have biodiversity and complexity akin to tropical rainforests (Raven, 2001, p. 155). However, in 1998, the United Nations Environmental Program suggested in its global assessment of reefs that 27% of the world's coral reefs are at high risk (Raven, 2001, p. 155).

Australia acted in 1975 to protect the Great Barrier Reef by passing the Great Barrier Reef Marine Park Act, which established the GBR Marine Park, the GBR Marine Park Authority responsible for management of the Park, and the GBR Consultative Committee to advise the Minister and the Authority. The Act provides a framework for planning and management of the Park, including zoning and management plans, and a permitting system for users of the Park. Also included was compulsory pilotage for certain ships in prescribed areas of the GBR region, collection of environmental management charges, and enforcement activities. Regulations were updated in 1983 to address provisions relating to offences, permits, pilotage, etc., again in 1999 to prohibit prospecting and exploration for minerals, and in 2000 to regulate the discharge of waste from aquaculture operations. Other Acts which protect the GBR include the Environment Protection and Biodiversity Conservation Act 1999, the Australia Heritage Commission Act 1975 (the Reef is included on the Register of the National Estate), the Environment Protection (Sea Dumping) Act 1981, and several other national and state legislative initiatives, along with a number of International Conventions, such as the Convention for the Protection of the World Cultural and Natural Heritage—1972, the Convention on Biological Diversity—1992 and the United Nations Framework Convention on Climate Change (Great Barrier Reef Marine Park Authority [GBRMPA], 2003).

In June 2003, Australia's Environment Minister David Kemp noted that "the Great Barrier Reef is the largest world heritage area in the world," and announced new zoning regulations for the Reef that "will establish a new international standard for the protection of reefs. The new regulations will bar fishing and shipping in nearly a third of the GBR, by expanding the "high protection zones" from 4.6 percent to around 30 percent, with only research and tourism allowed. Also, the "no-go" zones closed to all users except researchers with permits would be increased by about one-third. A spokesman for the GBR Marine Park Authority indicated that the greatest threats to the Reef come from sediment and chemical-laden runoff from coastal towns and farms, excess nutrients, overfishing by recreational and commercial fishers, and climate change that leads to coral bleaching (TerraDaily, 2003).

The World Wildlife Fund has recommended that because the Great Barrier Reef is home to six of the world's threatened turtle species, all known turtle nesting sites should be within marine sanctuaries, particularly their feeding areas. The WWF also suggests that a minimum of 50 percent of the GBR should be zoned as a marine sanctuary, and that according to a team of leading scientists, coral reefs "will not survive for more than a few decades unless they are promptly and massively protected from human exploitation" (World Wildlife Fund, Great Barrier Reef Campaign, 2003).

The GBR Marine Park Act provides a set of practical solutions to balance economic interests, environmental protection and scientific research needs. From the outset, a wide variety of stakeholders were involved in trying to identify the best protection methods, the areas of highest biodiversity, the greatest threats to survival of the GBR and Australia managed to create the protection network prior to widespread economic development. From the start, the scientific community participated in all decisions, and continues to share data and join in wide-ranging discussions on all matters of protecting the Reef. The role

Table 14-5. Summary of Great Barrier Reef Marine Park Zones (taken from Great Barrier Reef Marine Park Authority, Zoning, 2004).

Name of zone	General description
General Use A Zone	Least restrictive, allows for all reasonable uses, but prohibits trawling and general shipping.
General Use B Zone	Provides for reasonable use, including most commercial and recreational activities; prohibits trawling and general shipping.
General Use Zone	Provides for a diverse range of recreational and commercial activities.
Marine National Park A Zone	Allows appreciation and recreational use, including line fishing (one hook/person); spear fishing and collecting are prohibited, along with trawling and general shipping.
Habitat Protection Zone	Allows for a diverse range of recreational and commercial activities, but prohibits trawling.
Estuarine Conservation Zone	Protects estuarine areas free from loss of vegetation and disturbance, but allows for opportunities for commercial and recreational activities.
Conservation Park Zone	Allows for appreciation and enjoyment, including limited recreational fishing.
Marine National Marine Park B Zone	Provides for appreciation and enjoyment in undisturbed areas, a “look but not take” zone; fishing not allowed.
Marine National Park Buffer Zone	Usually 500 m wide provides for trolling for pelagic species around reefs where fishing is not allowed.
Buffer Zone	Protected areas, but allows mackerel trolling in areas adjacent to reefs zoned as National Park.
National Park Zone	Provides for protected areas of Marine Parks, a “look but not take” zone.
Scientific Research Zone	Set-aside exclusively for scientific research; entry and other uses prohibited.
Preservation Zone	Preservation in an undisturbed state; entry prohibited, except for research that cannot be conducted elsewhere.

of biotourism was always recognized as an important commodity to Australia, but not all reef zones allow for tourist activity. By maintaining a strict and thorough permitting system, with strong enforcement, the Park Authority is not only able to protect the reef, but also to maintain a dynamic database and provide for ongoing monitoring of the Reef’s health.

The Great Barrier Reef is zoned into 13 zones, intended to separate activities that might conflict with one another, and also allows areas that need permanent conservation to be placed off-limits to users (except scientific research) for varying lengths of times. Within the zones, there is provision for activities that are *as-of-right*, *with permission*, or *prohibited* (GBRMPA, 2004a). Table 14-5 provides a summary of the zones within the GBR Marine Park.

Permits may be needed for any activity to be undertaken in the Marine Park (depending on the zone), but in general, permits would be needed for commercial activities, tourist operations, installation and operation of all structures, dredging and dumping, creation of moorings, waste discharge from a fixed structure, research, educational programs and traditional hunting (GBRMPA, 2004b). Assessment and approval of a permit takes into account the objectives of the zone, cultural and heritage values, future impacts of the activity, conservation of natural resources of the Marine Park, effects on adjoining areas, the means of transport, arrangements for making good any damage brought about by the activity, and for costly projects, the financial capacity to complete the project (GBRMPA, 2004B). All scientific permit applications are submitted to the Park Authority, and are reviewed by aboriginal representatives, as well as by scientific review boards, and the permits usually remain active for one year. Applications are web-based, but must be submitted at least 90 days before the research commences, in order to allow for the different levels of review. All researchers must specify exact protocols, removal of species is strictly limited, and species data must be submitted to the Park Authority.

Given the size and complexity of the Great Barrier Reef system, the Marine Park Authority has been designed in a practical, yet detailed, manner, and there are several lessons that we can learn from review of the conservation effort:

- Conservation management plans must address conflicts among users of a natural resource area, particularly when one use may preclude another (e.g., trawling and reef conservation);
- International attention that is brought to a natural heritage site can help in creating conservation plans and implementing protection programs;
- Zoning can be utilized as a very effective management tool, especially if there are many stakeholders involved in setting up the zones; and
- Permit systems can be implemented whereby resource users can be restricted and monitored in an effective manner.

9.3. Recent Efforts in China to Address Environmental Protection and to Preserve Giant Panda Habitat

Since the *Metasequoia* Conservation Plan has an identified goal to establish protective reserves, and a commitment to work with Chinese national and local government officials, it might be valuable to consider recent efforts in China to address environmental degradation and resource protection. China has made considerable progress in curbing greenhouse gases, controlling population production, improving energy efficiency and expanding reforestation (Jing, 2002). Gao Guangsheng, Director of the Office of National Coordination Committee on Climate Change, reported at the World Summit on Sustainable Development, held in South Africa in October, 2002, that “the majority of ministerial departments in China have joined in the fight.” Gao also noted that “between

1998 and 2002, China earmarked a total of 580 billion yuan (US$70 billion) for environmental protection, some 1.29 percent of its gross domestic production (GDP) during the same period" and that China has approved the Kyoto Protocol as part of its efforts to combat environmental degradation (China Daily, 2003).

As a policy component in its environmental protection programs, China has moved aggressively forward in its efforts to expand hydroelectric power, with 19 currently operable hydroelectric projects with capacities greater than 1 gigawatt, projects under completion that will net at least 32 gigawatts of power, and other proposals for projects for a total of more than 16 gigawatts. In addition, the 18.2 gigawatt Three Gorges Dam is entering Phase 3 of completion, and will eventually extend 1.4 miles across the Yangtze, will be 607 feet tall, and will create a 370-mile-long reservoir. Concerns about the effects of the Three Gorges Dam include the potential for sedimentation of the river upstream of the dam, the required relocation and resettlement of millions of residents, the loss of archeological sites, and the loss or degradation of habitat of several endangered species and rare plants (Energy Information Administration, p. 9, 1999).

According to the official Xinhua News Agency in China, experts from the Chinese National Meteorological Center, and the Hubei provincial and Chongqing municipal meteorological stations in central and southwestern China conducted a seven-year weather simulation experiment. Their findings suggested that winters will become warmer and summers cooler (Environment News Service [ENS], 2002; Fackler, 2002). "The weather changes around the Three Gorges reservoir on the Yangtze River, will be greater in summer" and "... will include a moderate increase in rainfall." It is expected that the "extreme highest temperature near the reservoir will fall by 4°C, while the extreme lowest temperature will rise by 3°C." The forecasters also suggested that the rise in humidity might lead to more foggy days, and "the increase in vapor and fog will cause more frequent acid rains, which may move from urban areas to the countryside due to rising wind speeds" (ENS, 2002). It is possible that these climatic changes and ecological impacts may affect the native *M. glyptostroboides* populations, depending upon the extent of the change.

China is also developing other renewable resources. More than 140,000 mini-wind turbine units (60 to 200 watts) were operating in China in 1999, with expectations that the installed capacity of mini-wind turbines will be 140 megawatts, with total power generation of 450 gigawatt-hours, by 2020. China is also developing more geothermal heat resources to supplement its electrical production (Energy Information Administration, p. 10–11, 1999).

In addition to expanding renewable energy technologies as a means of reducing carbon dioxide, and the implementation of extensive reforestation programs (as discussed earlier), China has also developed programs for protecting endangered species, particularly the Giant Panda (*Ailuropoda melanoleuca*), an animal that has captured global attention. In 2001, the number of nature reserves throughout China had almost doubled in six years (1,551, compared to 793 in 1995), with state level natural reserves also showing an approximate twofold increase, from 98 in 1995, to 171 in 2001 (CIIN, 2003d). The "*Program of Action for Sustainable Development in China in the Early 21st Century*" identifies the need for protection of forest resources, including the need to "implement on a full scale key projects of protecting natural forests (CIIN, 2003e). The broad-based environmental protection efforts of the Chinese government, and particularly the commitment to save endangered species, suggest that efforts to protect *Metasequoia* might also be successful, if a compelling case could be made about the role of *Metasequoia* as part of the Chinese natural heritage, and the significance of this living fossil as a national treasure to be preserved for future generations. Therefore, it might be instructive to take a closer look at the extent of China's efforts to save Giant Panda habitat.

The Giant Panda is considered to be a specialist species, one with a narrow niche, (comparable to the Koala in Australia, or the Spotted owl in the Pacific northwest of the U.S.), feeding almost exclusively on various types of bamboo, eating one third of its body weight each day. Prices up to $176,000/pelt in Hong Kong or Japan create a strong economic pressure for capturing Giant Panda (Animal Diversity Web, 2003; Ward & Kynaston, 1995). Detailed studies of the Giant Panda in the 1980's focused on three distinctly different bamboo forest ecosystems, located at the Wolong Reserve in the Qionglai Mountains of Sichuan Province; the Tangjiahe Reserve in the Min Mountains of Sichuan Province; and the Foping Reserve and Chongqing Forest Bureau area of the Zinling Mountains of Shaanxi Province; research is continuing on bamboo ecology in Wolong and Tangjiahe Reserves (Jien, 1991). Although it is thought that the Giant Panda once lived in lowland areas, farming, forest clearing, and other development now restrict the bears to the mountains (China Daily, 2003).

China's efforts to protect the Giant Panda began in 1957, and the first four panda reserves were established in 1963. A Giant Panda Management Plan was designed by China's Ministry of Forestry and the World Wide Fund for Nature, to maintain a viable wild populations of Giant Panda as an integral part of China's Natural Heritage (Menghu & Tieqin, 1989). In 1992, the government passed the National Conservation Program for the Giant Panda and Habitat (Animal Diversity Web, 2003). By 1994, panda reserves comprised a total area of 5,827 km^2 in China, and today there are 33 reserves for protection of the Giant Panda (World Wildlife Federation [WWF], 2003). Habitat restoration is planned for some regions essential to the survival of the Giant Panda, and forestry practices will be modified in regions outside the reserves to bring about more sustainable timber operations (San Simon, 2003).

The Chinese government has passed anti-poaching laws to protect wild populations, with a penalty of death for trading panda skins; and has stopped commercial logging in these regions (Animal Diversity Web, 2003). An education program was started in 1986, reaching 5,000 villages, aimed at teaching farmers and villagers about panda protection, and discouraging them from cutting bamboo.

An estimated 1100 Giant Panda survive in the wild, in isolated "habitat islands" of bamboo forest in southwestern China, in the provinces of Sichuan, Shaanxi and Gansu, according to the second Giant Panda national survey (China Daily, 2003). One of these, The Wanglang Natural Reserve, established in 1963 to protect the Giant Panda, is located north of Chengdu, in the Minshan Mountains, which range in elevation from 2,430 to 4,980 m. These mountains are in the transition zone between the Qinghai-Tibetan Plateau and the Sichuan Basin. There are an estimated 30 wild pandas living in Wanglang, in thick bamboo groves. The Wanglang Reserve also protects other wildlife in the area, including three threatened species, the golden Snub-nosed monkey (*Rhinopithecus roxellarae*), the Takin (*Budorcas taxicolor*) and the leopard (*Panthera pardus*) (Wanglang Natural Reserve, 2003).

Giant Panda have a low birth rate, with only about one cub/female surviving each year, which must be cared for up to 22 months after birth. Additionally, pandas are selective about mates. Furthermore, bamboo dies off in cycles of 15–20 years, and takes years to reach edible size. Normally, pandas would migrate to another area, but with limited protected reserves, this may not be possible (Miller, 1998, p. 131). China's human population has soared, people trying to survive have pushed the pandas into smaller and smaller areas in the country's western mountains. The remaining pandas are confined to islands of forest dominated by a few bamboo species. When the plants have a setback, the pandas have no food source, and no alternative locale (Miller, 1998, p. 131). This cycle of distress continues to reduce the panda populations.

Habitat loss and fragmentation has constituted a major threat to the Giant Panda (Miller, 1998, p. 131), with populations often numbering less than 50 individuals in each isolated reserve (Yale Bulletin & Calendar, 2001). The key to the long-term survival of the Giant Panda "lies in the land outside the existing reserve system" (WWF, 2003). Two new land protection policies will be helpful in this regard, China's National Forest Conservation Program (NFCP) and its Grain to Green policy (WWF, 2003; Yale Bulletin & Calendar, 2001). However, the Western Development Program, which calls for expansion of hydropower generation, ecotourism development, and international investment, will tax this already burdened region, according to Lu Zhi, a researcher and visiting faculty member at Yale's School of Forestry & Environment and Associate Professor at Beijing University (Yale Bulletin & Calendar, 2001). Tourism would bring more hotels, roads, and visitors along with needed infrastructure for supplying food, water, electricity, waste disposal, etc.

A needed improvement is to create corridors for panda migration between adjacent reserves, where this would be feasible, and to educate local residents about the value of conserving pandas (Wanglang Natural Reserve, 2003; Yale Bulletin, 2001). Additionally, support of economic development in local communities may help to reduce pressure on panda habitats. The Giant Panda could face extinction through inbreeding, if the animals remain confined solely to existing nature reserves (WWF, 2003).

About 220 Giant Panda are found in zoos and research centers in China and elsewhere, but more captive pandas die than are born (Miller, 1998, p. 131). Improvements to captive breeding programs are planned, so that no more individuals are removed from the wild, and any surplus captive-born animals may be returned to the wild (San Simon, 2003). In 1984 the U.S. Fish and Wildlife Service listed the Giant Panda as an endangered species, under the Endangered Species Act of 1973, and the species is protected under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), a treaty signed by more than 140 nations. The U.S. Fish and Wildlife Service is the federal agency responsible for compliance with the CITES treaty, and oversees the importation of the Giant Panda for zoos and other breeding programs (San Simon, 2003). The Giant Panda has been designated by the World Conservation Union Red List of Threatened Animals, and is considered one of the most critically endangered creatures in the world (China Daily, 2003). From this summary, it is clear to see that the Chinese government has made a large commitment to saving an endangered species from extinction, has developed an extensive network of laws and restrictions over panda capture and killing, and has embarked upon a program of research and monitoring of panda habitat and ecology. Perhaps we can use the lessons learned from this endeavor to look for guiding principles in structuring the *Metasequoia* Conservation Plan.

9.4. Lessons Learned from China's Efforts to Preserve the Giant Panda

Ecosystem destruction produces cascading effects (e.g., deforestation may cause undue pressures on highly selective species such as the Giant Panda):

- Beautiful creatures capture the imagination of the world's children, thus building global support for protection programs;
- Gifts to zoos, matched with a controlled breeding program, can help to provide additional genetic stock, at least as an interim strategy;
- Need for ecosystem management, paired with community education programs;

- Isolated populations (located on "islands of habitat") may need access to one another, to assure reproductive success (need for green corridors);
- Don't wait too long, so that the resource is no longer sustainable ;
- Be careful about targeting ecotourism as a revenue generator to fund conservation programs (development impacts may outweigh economic benefits);
- Scientific investigations into the ecology of the Giant Panda and its habitat helped to make the protection programs more likely to succeed;
- It is possible to develop national programs in China that are partnered with international NGOs, and tailored to fit local community dynamics.

10. CONCLUSIONS

The native populations of *M. glyptostroboides* in China are in need of protection, and clearly from the foregoing discussion, there are ample models for how to implement the *Metasequoia* Conservation Plan that has been suggested in this chapter. By using the lessons learned from conservation efforts for the California redwoods, tropical rainforests, the Great Barrier Reef and the Giant Panda, we can move forward quickly and effectively to initiate the Conservation Plan. Action should be taken immediately to implement the various elements of the Conservation Plan, and to coordinate scientific investigations, policy planning, community action, and fundraising. This is an exciting opportunity to save this living fossil, *M. glyptostroboides*, before it disappears from the earth entirely.

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13. APPENDIX A

Example of an Endangered Species Conservation Plan

The United States Endangered Species Act provides detailed guidelines for identification of threatened and endangered species, and for developing a conservation plan to protect that species. Elements of a Conservation Plan for a protected species in the United States would typically include the following components:

1. Identify potential conservation sites;
   - Scientists must determine feasibility and environmental constraints, and then set scientific goals;
   - Local and regional officials must review the sites and minimize impacts on local citizens, resulting in the least change in lifestyle;
   - Present and future value must be assessed;
2. Create a management scheme;
   - Map site and its surrounding land uses;
   - Identify of all permits needed;
   - Determine a stewardship strategy, including as many stakeholders as possible;
   - Develop penalties for failure to follow the Conservation Plan;
3. Develop a funding scheme to support Conservation Plan;
   - Identify role of private donors;
   - Assess potential for government funding;
   - Determine fee schedule (if needed);
4. Develop Education Program;
   - Design curriculum packages to heighten awareness and report progress;
   - Develop training programs for stewards, educators, and other stakeholders;
5. Design Marketing Plan;
   - Determine funding sources to be targeted;
   - Identify government decision makers who can act as champions for the project;
   - Approach scientists for proposals for site/field studies designed to meet the project goals;
   - Recruit teachers as site interpreters and for curriculum development;
   - Alert the general public on the values and goals of the protection program;
6. Develop a communication improvement plan.

This procedure was used for protection of a rare wetland plant found in Rhode Island, the Swamp bulrush (*Schoenoplectus etuberculatus* (Steud.) Sojak. This plant has specifically been identified as a Division I species in *Flora Conservanda: New England* (Brumback & Mehrhoff *et al.,* 1996; Enser, 2002). This designation indicates that the swamp bulrush is "a globally rare species as defined in the ranking system derived by the Nature Conservancy to identify species of particular conservation concern" (Enser, 2002). Within this ranking system, *S. etuberculatus* is ranked as a G3G4 taxon, a species that may be rare or uncommon, but not imperiled globally (Enser, p. 1). Recognizing the need to "identify conservation and management objectives" for protecting this species, a "Conservation and Research Plan" has been prepared, as part of the New England Plant Conservation Program of the New England Wildflower Society (Enser, 2001).

Conservation actions recommended for this site include landowner contact, working with local officials to limit passive recreation (nature walking and fishing). Additionally monitoring of the *S. etuberculatus* population should continue, to assess potential impacts from the spread of invasive plants and grazing of plants by waterfowl (Enser, 2002).

Potential research efforts include genetic analysis of *S. etuberculatus* throughout its range, to determine the uniqueness of this population. If this single population were genetically distinct,

Table 14-A1. Conservation ranking system for a protected species

Ranking	Condition
1	Critically imperiled
2	Imperiled
3	Vulnerable to extirpation or extinction
4	Apparently secure
5	Demonstrable widespread, abundant, and secure

the plant would be assigned a higher conservation priority. Studies of the relationship between water levels and plant reproduction are also recommended, along with an assessment of the use of this species as food for waterfowl (Enser, 2002).

Seeds of *S. etuberculatus* have been collected and are maintained at the New England Wild Flower Society (NEWFS). Representative samples should be periodically tested for viability, with resulting plants maintained in the NEWFS Garden of Rare and Endangered species (Enser, 2002).

In terms of education, local officials and private landowners in the vicinity should be notified of this and other rare species. Managers of a nearby local recreation facility should be consulted regarding future activities, including siting of nature trails and fishing access. A bathing beach is discouraged. Consultation with landowners should focus on maintaining the integrity of the shoreline, with natural vegetation left in place (Enser, 2002).

The Nature Conservancy maintains a conservation ranking system, ranging from 1 to 5, preceded by a G (global), N (national), or S (subnational) as appropriate. The lower the number, the higher the conservation rank (Table 14-A1).

G1, for example, indicates critical imperilment on a range-wide basis, that is, a great risk of extinction. Species known in an area only from historical records are ranked either H (possible extirpated/possible extinct), or X (presumed extirpated/presently extinct). The ranking system makes it easier to set appropriate conservation priorities in different places and at different geological levels (Enser, 2002).

Ranking is a qualitative process; it takes into account several factors, including total number, range, population size, range extent, and area of occupancy, short- and long-term trends, threats, environmental specificity, and fragility. These factors function as guidelines (Enser, 2002, Appendix 2).

14. APPENDIX B

Sample Curriculum for Metasequoia Education Program

I. Feelings/Contact with Nature

> *"If a child is to keep alive his inborn sense of wonder, he needs the companionship of at least one adult who can share it, rediscovering with him the joy, excitement and mystery of the world we live in." Rachel Carson*

Most people seem to fall in love with the Earth through direct exposure to its elements, through firsthand contact with nature, usually as a result of their childhood experiences. The *Metasequoia* Education Program should include activities that focus on this connectivity, and might include some of the following exercises:

- Finding a magic spot to feel the flow of life;
- Listening to birds and insects with eyes closed;
- Seeing the world from an insect's point of view;
- Hiking or orienteering in the forest;
- Walking along a "touching trail" (with a "helper");
- Painting the special sights in a forest;
- Creating micro-parks at ground level;
- Pressing fallen leaves;
- Listening to the sap flow through a tree (with a stethoscope).

II. Ecological Knowledge Base

The following topics would be essential concepts underlying a *Metasequoia* Education Program, but other specific biological and genetic aspects might also need to be included:

- Flow of energy;
- Cycling of Matter;
- Water Cycle;
- Oxygen/Carbon Dioxide Cycle;
- Food Webs;
- Concept of Niche and Ecological Specialization;
- Changes in Forests (Ecological Succession);
- Ecology of *M. glyptostroboides* Forests (including characterization of the biota of a typical *M. glyptostroboides* forest).

III. Principles of Sustainability

To better appreciate the plight of the native *M. glyptostroboides* forests, and the challenges of truly preserving their threatened existence, stakeholders must have a deep understanding of the principles of sustainability for protecting biodiversity and maintaining vital and dynamic ecosystems. This challenge would necessitate inclusion of the following principles:

- Protecting the earth for future generations;
- Maintaining the cycles of nature;
- Understanding the importance of biodiversity;
- Improving energy efficiency for all human activities;
- Limiting human population growth;
- Developing better techniques for materials management;
- Adopting the concept of natural capital as an essential component of human system.

IV. Threats to Metasequoia glyptostroboides Forests in China

Since there are specific dynamics that have led to the reduced distribution of the once-plentiful *M. glyptostroboides* forests (some natural limitations and some manmade disturbances), it will be important to include these in the curriculum for the education program. Some issues to be considered are listed below:

- Lost habitat, some of which is wetlands;
- Conflicts associated with needed agricultural land;
- Ecological competition with bamboo and other fast-growing plants;
- Insect pests and appropriate Integrated Pest Management programs;
- Limited genetic diversity and low seed viability in small populations;
- Harvesting of fuel wood for individual and/or industrial use
- Industrial activities;
- Wood used for making charcoal;
- Generation of air pollution;
- Climate change;
- Reduced or increased rainfall;
- Changes in the ambient temperature regime;
- Lack of knowledge regarding the ecological and evolutionary significance of *M. glyptostroboides*.

V. Need for Community Involvement and Protection

A *Metasequoia* Conservation Plan cannot be adopted without having the enthusiastic support of all stakeholders. It is equally important that all stakeholders understand the importance of this collaboration, so the concepts and strategies for accomplishing local involvement should be included in the Education Program, including the rationale underlying the following concepts:

- Part of the natural heritage of China;
- A "living fossil" in need of preservation;
- An endangered species ;
- Part of the world's biodiversity;
- Local residents have stewardship responsibilities;
- Qualification of the species for funding from several United Nations programs.

VI. Development of Case Studies

Case studies are important tools for broad distribution of information about the biology, genetics, evolution, and policy of an endangered species, and the Education Program should include the development of appropriate case studies for different fields of study. Some examples are listed below:

- Loss and preservation of native *M. glyptostroboides* forests;
- Preservation of redwoods in California;
- Studies of *M. glyptostroboides* worldwide;
- Corporate support of endangered species protection;

Other components of the *Metasequoia* Education Program can and will be added as the program continues. Graduate students in Education degree programs could be enlisted to expand and refine these programs.

15. APPENDIX C

Potential Sources of Financial or Technical Support

1. Conservation Funding for Forests: Funding provided for forest preservation. http://www.bothends.org/service/forestfunds2003.htm#Ancient%20Forests%20International
2. Conservation International (CEPF): Critical Ecosystem Partnership funds Safeguard biodiversity hotspots and builds capacity for local implementation of conservation projects and assists in the regional planning authorities with conservation. This program is involved with expanding the distribution of restoration programs for China's natural vegetation. http://www.cepf.net/xp/cepf
3. Fauna & Flora International: Provides funding for conservation partnerships for plant propagation and ecological restoration. http://www.fauna-flora.org
4. JFGE: Funding provided for environmental conservation activities in developing regions by Japanese NGOs. Examples include reforestation of the southern part of Sri Lanka and tree Planting in the western corridor of the Yellow River in China. http://www.eic.or.jp/jfge/english/recipients/00orig.html
5. John D. and Catherine T. McArthur Foundation: Funding provided for ecosystem conservation and biodiversity protection. This foundation has funded several projects in Asia. http://www.macfound.org
6. Nature Conservancy: Support for international conservation projects such as the Greater China Program or the Hunan Great Rivers Program. http://www.natureconservancy.org
7. National Science Foundation (ERE Program): Funding provided for Environmental Education, Biocomplexity and International Activities with a focus on Environmental Education. http://www.nsf.gov/geo/ere/ereweb/fundlisting.cfm?09560946044806144F1D4B14484014
8. National Science Foundation (REU Program): Funds research opportunities for students. http://www.nsf.gov/home/crssprgm/reu/start.htm
9. United Nations Development Program: Broad-based funding for UNDP Global Environment Facility (UNDP-GEF) and small grants Program. http://www.undp.org.gef
10. United Nations Environment Program: Broad-based funding for UNEP World Bank. http://www.undp.org.gef
11. Toyota Company: Cooperation with Society Social Contribution activities for reforestation activities in China. http://www.toyota.co.jp/Irweb/corp_info/eco/beyond07.html or Environmental Activities Grant Program. http://www.toyota.co.jp/Irweb/corp_info/eco/grant.html
12. W. Alton Jones Foundation: Funding to maintain biological diversity and avoid contamination. The Sustainable World Program is one example of the benefits of the funding provided by this foundation. http://ww.gm-unccd.org/FIELD/Foundations/Jones/FR_Gr.htm
13. World Conservation Union (IUCN): Funding provided for land conservation and wetlands protection. http://www.iucn.org/ourwork/asia.htm
14. World Wildlife Fund: Provides funding for forest and habitat protection programs such as the Forest Partnerships (Alliance with the World Bank). http://www.panda.org/about_wwf/what_we_do/forests/what_we_do/partnerships/index.cfm or http://lnweb18.worldbank.org/essd/envext.nsf/80ByDocName/AllianceActivitiesAroundTheWorld

16. APPENDIX D

Establishing a Nonprofit Organization in the United States

http://www.fdncenter.org/learn/classroom/establish/index.html

An effective non-profit organization is described by the Grantmakers for Effective Organizations, a group associated with the Council on Foundations, as having "the ability to fulfill its mission through a blend of sound management, strong governance, and a persistent rededication to achieving results" (The Foundation Center, 2002). The characteristics of a nonprofit organization include the following:

- Vital mission;
- Clear lines of communication;
- High level of accountability and public transparency;
- Adequate facilities and infrastructure;
- Reliable and diverse revenue streams; and
- High quality programs and services

Tutorials are available online, which detail the tasks to be completed in the process of establishing a 501-C-3 nonprofit organization (The Foundation Center, 2002).

17. APPENDIX E

International Forest Organizations and Agencies*

- All Species Foundation http://www.all-species.org/http://www.all-species.org/
  - Nonprofit organization
  - Goal of complete inventory of all species within next 25 years
- Asia-Pacific Association of Forest Research Institutes (APAFRI)
- Center for International Forestry Research (CIFOR)
  - Coordinates research to find underlying causes of deforestation and degradation
  - Strengthen forest policy at the global level
- Collaborative Partnership on Forests (CPF)
  - Provides expertise and information
  - Mobilizes financial resources
  - Networks with a wide range of partners (FAO, CBD, UNEP, World Bank)
- Convention on Biological Diversity (CBD)
  - Program of Work on Forest Biological Diversity
- International Union of Forestry Research Organizations (IUFRO)
  - Comprised of 15,000 scientists from 700 institutions in 112 countries; established 110 years ago, deals with broad-based issues
- National Forest Program Facility Collaboration
  - Focuses on information exchange, knowledge sharing, and capacity building
  - Improving conditions that foster sustainable forest management
  - Link forest policy and planning with broader national objectives
- Ramsar Convention on Wetlands
- United Nations Forum on Forests
  - Established in 2002 to carry out the mandate of IPF (Intergovernmental Panel on Forests) and IFF (International Forum on Forests)
  - Develop a legal framework covering all types of forests
  - Focus on issues related to financial and technological support for implementing sustainable forest management
  - Focus on combating deforestation and degradation, and of conserving and protecting unique types of forests
- World Summit on Sustainable Development
  - Sets up international partnerships, such as the Asia Forest Partnership
  - Develop forest policies, plans and programs
  - Encourage use of satellite data and mapping
  - Exchange information and experiences
  - Identify and implement new multilateral programs

*Derived from information provided by UNFAO http://www.fao.org/DOCREP/005/Y7581e/Y7581E00.htm

18. APPENDIX F

Sample *Metasequoia* Fact Sheet*

Figure 14-1. Photo Courtesy of Ben LePage, 2002

History

The dawn redwood (*Metasequoia glyptostroboides*) is a deciduous conifer tree that can reach between 75' and 100' tall. In 1941, It was first discovered as a fossil in 1941 by the Japanese paleobotanist Shigeru Miki and later in 1948, it was discovered and described as new species of redwood from China.

From 100 million years ago to approximately one million years ago, the *Metasequoia* tree was widely distributed over the Northern Hemisphere. A small region in southeastern China is the only habitat left that is home to native populations of this tree. The dawn redwood naturally occurs in the Hubei region in southwest China, where about 5,400 trees remain.

Problems Facing Metasequoia glyptostroboides

The *Metasequoia* population lacks seedlings and saplings, implying that these trees are going extinct in their native habitat right before our eyes. The living trees that are in what should be their reproductive years are not producing useful seeds. This is possibly due to inbreeding depression. All of the trees now living in this region of China may have been derived from a single isolated population of tree or even from a single tree from Moudao. Due to their limited genetic diversity, the trees that are still alive are not breeding properly.

The tree grows poorly on dry, acidic soils and is susceptible to several insect pests. Also, its habitat is being encroached upon for farmland, and the trees themselves have been stripped of their branches for many years. The branches are used for firewood, or for roof thatching.

What You Can Do

- Plant *M. glyptostroboides* trees;
- Support *M. glyptostroboides* protection programs;

- Report anyone who is damaging or killing *M. glyptostroboides* trees;
- Be aware of the processes that may harm the habitat of *M. glyptostroboides*;
- Preserve *M. glyptostroboides* and its habitat.

*Adopted from a draft prepared by graduate students of Ben LePage at the University of Pennsylvania.

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