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The Ecology of Podocarps in Tropical Montane Forests of Borneo: Distribution, Population Dynamics, and Soil Nutrient Acquisition

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ABSTRACT. We review the ecology of podocarps on various soil types in Borneo, largely relying on our studies conducted on Mount Kinabalu. Podocarps are generally abundant in montane forests, but their abundance varies with soil nutrient status, and they can occur in lowland forests where soil nutrients are scarce. These patterns suggest control by soil nutrients rather than by temperature. Analyses of population structure, growth rate, and crown light conditions in montane forests indicate that podocarps are generally shade intolerant and require canopy gaps or sparse canopy for regeneration. Podocarps have greater maximum tree sizes than most co-occurring angiosperm species in Mount Kinabalu forests. Once they reach the upper canopy layer, they persist for a long time because of their long life span, allowing them to regenerate in rare events of canopy disturbance. The roots of two podocarp species (*Dacrycarpus imbricatus* and *Dacrydium gracile*) showed a greater acid phosphatase activity when compared with angiosperm roots within the same lower montane forest. Moreover, an analysis using lipid biomarkers indicated that saprophytic fungi are more abundant in the soils beneath the two podocarps than beneath angiosperms, and a fungal biomarker lipid correlated with soil acid phosphatase activity. The dominance of saprophytic fungi appears to be related to high soil acid phosphatase activity, suggesting feedback effects between the podocarps and soil microbial communities. These results indicate that podocarps are efficient in the acquisition of phosphorus from the acidic montane soils and decomposing litter. We suggest that the architectural and life history advantages and physiological adaptations to nutrient limitation are essential for the persistence of podocarps, despite their lower shade tolerance as compared to angiosperms.

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INTRODUCTION

The contemporary landscapes of Borneo are characterized by towering, evergreen broad-leaved tropical rainforests. Because the family Dipterocarpaceae is the dominant element, they are called mixed dipterocarp forest (Richards, 1996). The Gnetaceae, usually lianas, is the only gymnosperm family that is relatively common in such mixed dipterocarp forests. Because families in the Coniferales are virtually absent in mixed dipterocarp forests, plant ecologists may have the false impression that conifers are not physiologically adaptive to hot tropical climates. Richards (1996) illustrated that the Coniferales, including the Podocarpaceae, increases in abundance with increasing altitude in the paleotropics (Africa and South-east Asia, including New Guinea). Similarly, Veblen et al. (2005) stated that podocarps were generally restricted to montane cloud forests in tropical South America.

Although the patterns illustrated by Richards (1996) and Veblen et al. (2005) are real, they do not necessarily mean that the Podocarpaceae is a cool-climate element in the tropics, because soil nutrients may affect its distribution. There is a general trend in the tropics that lowland forests are limited by phosphorus availability and montane forests by nitrogen availability; in particular, soil nitrogen availability declines with increasing altitude, reflecting slower rates of mineralization (Tanner et al., 1998). Thus, it is not obvious that temperature, rather than nutrients, most strongly limits the distribution of the Podocarpaceae. In this review we illustrate the distribution patterns of the Podocarpaceae (and associated taxa) on various soil types in Borneo and suggest that they are controlled by soil nutrients more than by temperature. Our model site is Mount Kinabalu (Figure 6.1) in Sabah, a Malaysian state found in the north tip of Borneo.

Mount Kinabalu (4,095 m, 06°05'N, 116°33'E) is nonvolcanic and is the highest mountain in Southeast Asia between the Himalayas and New Guinea. The summit and adjacent areas are protected within the Kinabalu Park. Diverse pristine rainforests, which are all evergreen, occur from 300 m to the forest limit at 3,700 m (Kitayama, 1992a). The climate is humid tropical, with a weak influence of the Asiatic monsoon. Mean annual air temperature is 18.3°C at 1,560 m and decreases linearly with increasing altitude, with a mean lapse rate of 0.55°C per 100 m (Kitayama, 1992a). Month-to-month thermal seasonality is generally <2°C. Mean atmospheric saturation deficits become less negative upslope as a function of decreasing air temperature. Mean annual rainfall during 1994–1997 was approximately 2,300 mm at all altitudes. Longer-term

measurements may, however, demonstrate a much greater year-to-year variation in rainfall.

The geological substrates below 3,000 m consist of large areas of Tertiary sedimentary rocks with mosaics of ultramafic rocks (Jacobson, 1970). The folding of the sedimentary rocks occurred in the middle Miocene (15 MYA), and the ultramafic rocks were probably up-faulted into the sedimentary rocks at that time. The summit area above 3,000 m consists of granitic (adamellite) rocks. The intrusion of the batholithic granite through sedimentary rocks started in the upper Miocene (7–9 MYA), and the summit is still being uplifted. The ultramafic rocks are remarkably high in magnesium and low in phosphorus compared with sedimentary and granitic rocks found in the area.

Forest ecosystems of Mount Kinabalu were recently investigated intensively with permanent plots at various altitudes on different surface geologies (Kitayama et al., 1998, 2004; Aiba and Kitayama, 1999; Kitayama and Aiba, 2002; Takyu et al., 2002; Aiba et al., 2004, 2005, 2006, 2007; T. Seino and K. Kitayama, unpublished). Forest function, nutrient dynamics, and the populations of all trees >5 cm in diameter at breast height (dbh) were investigated (Table 6.1). In this paper, we review the results pertinent to the Podocarpaceae on Mount Kinabalu.

The genus *Phyllocladus* is included in Podocarpaceae in this paper (see Biffin et al., this volume), although it has been elevated to family level in some of the literature (Page, 1990; Bobrov et al., 1999). Podocarpaceae forms a monophyletic lineage with Araucariaceae within extant conifer families in the molecular phylogeny; both families possess nodulelike structures on roots and show a geographic distribution biased to the Southern Hemisphere, probably reflecting their Gondwanan origins (Quinn et al., 2002). All coniferous species occurring on Mount Kinabalu belong to these two families. We therefore include Araucariaceae (only the genus *Agathis* occurs in Borneo) in places because the two families are likely to share some common ecological characteristics owing to their common ancestry.

DISTRIBUTIONAL PATTERN

GENERAL ALTITUDINAL DISTRIBUTION

In the lower montane tropical rainforest at park headquarters (1,560 m) of Kinabalu Park, one can easily recognize slightly overtopping crowns of conifers by their fine texture (Figure 6.2). These conifers are likely to be either of the two abundant podocarps, *Dacrycarpus imbricatus* and *Dacrydium gracile*. The other dominant



FIGURE 6.1. Mount Kinabalu viewed from the park headquarters (1,560 m) on the south slope.

species include angiosperm trees of the genera *Tristaniopsis*, *Syzygium* (both Myrtaceae), and *Lithocarpus* (Fagaceae). Similar forests characterized by the dominance of conifers (especially podocarps) are seen in montane forests (subalpine, upper montane, and lower montane forests; Kitayama, 1992a) on Mount Kinabalu above the upper limit (1,200 m) of mixed dipterocarp forest. A total of 20 species of conifer (three Araucariaceae and 17 Podocarpaceae, including one *Phyllocladus*) have been recorded on Mount Kinabalu (Beaman and Beaman, 1998).

Conifers have long been considered an important “montane” floristic element on Mount Kinabalu (van Steenis, 1964; Meijer, 1965). Quantitative analysis of the vegetation on zonal soils from the lowlands to the upper limit of forest (600–3,400 m) supported this general

pattern: podocarps and other conifers were recorded only at $\geq 1,400$ m (Kitayama, 1992a). Podocarps were notably dominant from 2,800 to 3,400 m (Kitayama, 1992b), although the number of podocarp species peaked at 1,500–1,600 m (Beaman and Beaman, 1998). Therefore, at first glance, the distribution of podocarps appears to be controlled by climate (primarily by temperature).

Analyses of the altitudinal distribution patterns of trees on different geological substrates on Mount Kinabalu (Aiba and Kitayama, 1999), however, suggest that the occurrence of podocarps is, in reality, controlled by a more complex interaction of climate and soil conditions (Figure 6.3). The abundance of podocarps at a site generally increases with altitude, but it can vary from site to site depending on geology. As has been stated, on zonal

TABLE 6.1. Description of sample plots established on different geological substrates on Mount Kinabalu.

Exact elevation (m)	Area (ha)	Tree density (ha ⁻¹) ^a	Altitudinal zone ^b	Surface geology ^c	Topography ^d	Census year	Reference
Nonultramafic rock (zonal soil)							
650	1.00	1,055 ^e	L	T	S	1996	Aiba and Kitayama (1999)
1,560	1.50 ^f	1,921	LM	T	L	1997, 2002	Takyu et al. (2002), Kitayama et al. (2004), Aiba et al. (2006)
1,560	0.10	3,030	LM	T	M	1997	Takyu et al. (2002)
1,560	0.05	3,300	LM	T	R	1997	Takyu et al. (2002)
1,860	1.00	1,951	LM	Q	L	1996	Takyu et al. (2002), Kitayama et al. (2004)
1,860	0.10	2,450	LM	Q	M	1997	Takyu et al. (2002)
1,860	0.05	3,180	LM	Q	R	1997	Takyu et al. (2002)
1,950	0.50	1,624	LM	T ^g	V	2000	T. Seino and K. Kitayama (unpublished)
2,590	0.25	2,116	UM	T	S	1995	Aiba and Kitayama (1999)
3,080	0.20	3,665	SA	G	S	1995	Aiba and Kitayama (1999)
Ultramafic rock (azonal soil)							
700	1.00	1,195 ^e	L	S	S	1996	Aiba and Kitayama (1999)
1,860	0.20	3,445	LM	S	L	1995	Aiba and Kitayama (1999), Takyu et al. (2002)
1,860	0.10	4,190	LM	S	M	1997	Takyu et al. (2002)
1,860	0.05	4,100	LM	S	R	1997	Takyu et al. (2002)
2,700	0.20	3,775	UM	S	S	1995	Aiba and Kitayama (1999)
3,050	0.06	4,383	SA	S	S	1995	Aiba and Kitayama (1999)

^a Stems ≥ 5 cm diameter at breast height.

^b L, lowland; LM, lower montane; UM, upper montane; SA, subalpine zones (Kitayama, 1992a).

^c T, Tertiary sedimentary rock; Q, Quaternary sediment; G, granite; S, serpentine rock.

^d L, lower slope; M, middle slope; R, ridge top; S, side slope; V, valley bottom.

^e Estimates based on the entire plot (1 ha) for stems ≥ 10 cm diameter at breast height and subsamples (0.20 ha) for stems < 10 cm diameter at breast height.

^f A single 1-ha plot censused in 1997 and two 0.25-ha plots censused in 2002.

^g The surface geology of this site appears to include various rock types (Quaternary sediment and ultramafic rock), although the site is mapped within an area of Tertiary sedimentary rock in Jacobson (1970).

soils derived from sedimentary or granitic rocks, the genera *Dacrycarpus* and *Dacrydium* are the dominant podocarps in the most developed forests on gentle slopes in the montane zone or above. Podocarps, which are otherwise exclusively montane, occur at a lower altitude of 700 m on soils derived from ultramafic rock, suggesting that soil conditions can strongly influence their distribution. The phylogenetically associated family Araucariaceae (*Agathis borneensis* in lowland forests and *A. kinabaluensis* in montane forests) also demonstrates a staggered, lowered altitudinal distribution on soils derived from ultramafic rock.

Podocarps and *Agathis borneensis* can occur at sea level in Borneo on sandy or swampy soils (de Laubenfels, 1988; Miyamoto et al., 2003; Nishimura et al., 2007). A low-stature evergreen forest, consisting of slender gnarled

trees, occurs on nutrient-impooverished, sandy Spodosols (Soil Survey Staff, 1999), and the forest is termed "heath forest." In the southwestern lowlands of interior Sabah, *Dacrydium pectinatum* is among the dominant species of heath forest at 500 m (Figure 6.4). The relative basal area of *Dacrydium* can exceed 40%, and Myrtaceae and Dipterocarpaceae compose the bulk of the rest in this forest (K. Takahashi and K. Kitayama, Kyoto University, unpublished data). This again suggests that the altitudinal distribution of podocarps is "lowered" on nutrient-impooverished soils.

All of the podocarp species (as well as *Agathis* species) have broad altitudinal ranges on Mount Kinabalu. *Dacrycarpus imbricatus* was once believed to occur from 1,400 up to 4,000 m. After a taxonomic revision, however, the



FIGURE 6.2. The canopy of lower montane tropical rainforest on Mount Kinabalu at 1,560 m, where several of the studies described in this chapter were conducted. This forest is dominated by *Dacrycarpus imbricatus* and *Dacrydium gracile*.

plants at the upper slope were split as an endemic species, *D. kinabaluensis*. The latter species occurs most abundantly (with 5% relative basal area or greater) at altitudes higher than 2,800 m on both ultramafic and sedimentary rocks (Kitayama, 1992a; Aiba and Kitayama, 1999). Five species of *Dacrydium* occur between 800 and 3,700 m (Beaman and Beaman, 1998; although occurrence of one species is questionable). *Phyllocladus hypophyllus* also occurs widely from 1,200 up to 4,000 m. These distribution patterns suggest that podocarps have potentially wide physiological ranges. Three species of *Agathis* (Araucariaceae) are recorded from the somewhat narrower range from 800 to 2,200 m.

Although podocarps (the genera *Dacrycarpus* and *Dacrydium* in particular) have a potentially wide altitudinal range, there is a distribution gap between 2,000 and 2,800 m on gentle slopes on sedimentary soils (corresponding to the upper montane tropical rainforest) where *Dacrycarpus* does not occur (Kitayama, 1992a). Aiba and Kitayama (1999) also found only one podocarp species (*Phyllocladus hypophyllus*) in an upper montane cloud forest on sedimentary soils at 2,590 m. The soils in the upper montane forest are commonly waterlogged and chemically reduced because of persistent cloud and rainfall and may be too wet for the other conifers. Indeed, podocarps can frequently occur on steep ridges on sedimentary rock

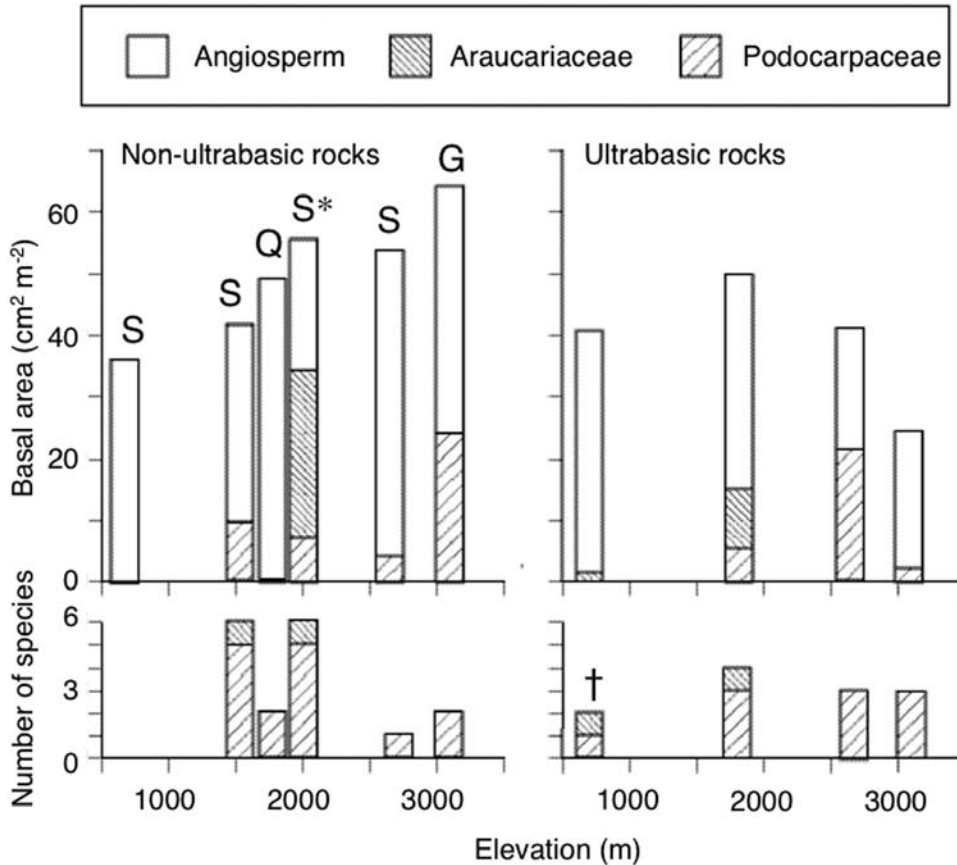


FIGURE 6.3. (top) Basal area and (bottom) number of species of conifer families (Podocarpaceae and Araucariaceae) for trees ≥ 5 cm diameter at breast height in sample plots on side slopes (including lower slopes and valley bottom) established on two geological substrates along elevational gradients on Mount Kinabalu. The basal area of angiosperm trees combined is also shown. Rock types are indicated for nonultramafic series as follows: S = Tertiary sedimentary rock, Q = Quaternary sediments, G = granite. The surface geology of the site indicated by an asterisk (*) may include various rock types; see footnote g of Table 6.1. The number of species for the plot at 700 m on ultramafic rock [indicated by a dagger (†)] includes one podocarp species that occurs just outside the plot (*Dacrycarpus imbricatus*).

or gentle slopes on ultramafic rock in this zone (Kitayama, 1995). At these sites, water permeability is high because of steep topography and, on ultramafic soils, the presence of iron oxides, which have a low affinity with water. *Dacrycarpus* gains dominance in the slightly drier subalpine zone ($\geq 2,800$ m), which is above the persistent cloud. *Dacrydium* occurs in low abundance in the lower montane zone but does not occur in the upper zone except on ridgetops and ultramafic soils. As explained above, podocarps do occur on waterlogged soils elsewhere in Borneo, and we do not know why they are absent from such soils on Mount Kinabalu.

Although conifers co-occur with angiosperms, the “additive basal area phenomenon” (Enright and Ogden, 1995; Aiba et al., 2007) is not evident on Mount Kinabalu. This phenomenon is often reported for mixed conifer–angiosperm forests in the Southern Hemisphere, in which the high basal area of conifers does not cause the reduction of basal area of angiosperms.

RESPONSE TO VARIATION IN SOIL NUTRIENTS

The above description suggests that soil conditions rather than climate may impose the main control



FIGURE 6.4. Heath forest on white silica sands in the interior of Sabah, north Borneo, at 500 m. *Dacrydium pectinatum* is the dominant species in this nutrient-impooverished forest.

on the occurrence of podocarps and other conifers on Mount Kinabalu. Variation in podocarp abundance appears to be correlated with net soil nitrogen mineralization rate (Figure 6.5). Takyu et al. (2002) investigated tree species composition in nine lower montane forests at 1,560–1,860 m on Mount Kinabalu, including ridge, middle-slope, and lower-slope forests, each occurring on unconsolidated Quaternary sediment (colluvial deposits of sedimentary rocks), Tertiary sedimentary rock, and ultramafic rock (Table 6.1). Soil nitrogen availability generally decreases from Quaternary to Tertiary to ultramafic (most nutrient deficient) and from lower slope to middle slope to ridge (most nutrient deficient) on each substrate.

With this combination of site conditions, the abundance of podocarps generally decreases with increasing nitrogen availability ($r = -0.47$, $p = 0.203$), significantly so when all conifers (including *Agathis*) were included ($r = -0.67$, $p = 0.049$). It has been demonstrated that soil phosphorus availability also changes with geological substrate and topography in a manner similar to soil nitrogen (Kitayama and Aiba, 2002; Kitayama et al., 2004). Therefore, nitrogen in concert with phosphorus may be important in determining the abundance of podocarps and other conifers in the lower montane zone of Mount Kinabalu.

Kitayama et al. (2004) compared soil phosphorus availability in two lower montane tropical rainforests with

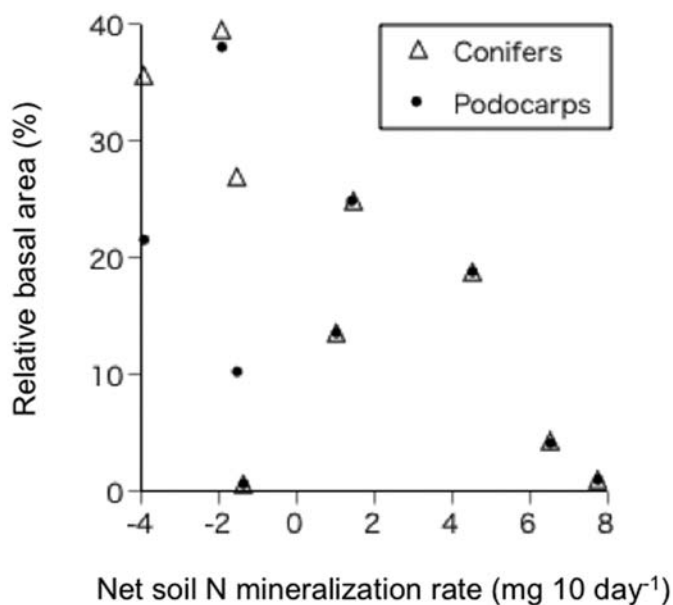


FIGURE 6.5. The relationships between net soil nitrogen mineralization rate and the relative basal areas of podocarp and conifer species in nine tropical rainforests of the lower montane zone on Mount Kinabalu. Net soil nitrogen mineralization rate was determined by 10-day incubation of forest soils in polyethylene bags (Takyu et al., 2002).

similar air temperature regimes but on different geological substrates: highly weathered soils on stable, old Tertiary sedimentary rocks and undeveloped soils on unconsolidated Quaternary sediment (Table 6.1). Concentrations of labile and total phosphorus were much lower in the old soils and appeared to control primary productivity. Podocarps are among the dominant trees in forests growing on old soils but are very rare in the forest growing on young soils, suggesting that phosphorus availability alone or in concert with nitrogen availability controlled the occurrence of podocarps at these sites.

POPULATION ECOLOGY IN MONTANE FORESTS

DIAMETER DISTRIBUTION

In the montane (and subalpine) forests on Mount Kinabalu, podocarps and the associated conifer *Agathis kinabaluensis* do not necessarily appear to be competitive with angiosperm trees in terms of aboveground competition for light. Figure 6.6 demonstrates the diameter size

class distribution of conifers (podocarps and *A. kinabaluensis*) and angiosperm trees in three upland forests on zonal soils derived from sedimentary or granitic rocks and two forests on soils derived from ultramafic rocks. Conifers are minor elements in terms of the number of stems, but they constitute a substantial fraction of large-sized stems, resulting in a relatively large basal area (Figure 6.3). Individual conifer species usually show flat or monomodal diameter distributions with few small trees, which indicates that they are shade intolerant (Figure 6.7). Occasionally, some conifers show an L-shaped diameter distribution with abundant small trees. However, the canopy layers in such forests are sparse, which allows smaller conifer trees to persist in the understory layer. These cases are rather rare. *Dacrycarpus kinabaluensis* found at 3,080 m on granite showed extremely unimodal diameter distribution, which might reflect an episodic recruitment following large-scale disturbance (e.g., El Niño-related drought or landslides). *Falcatifolium falciforme* at 1,560 m on sedimentary rock is exceptional in that it shows clearly an L-shaped diameter distribution and saplings grow abundantly in shaded conditions of the forest understory (see below).

DIAMETER GROWTH RATE AND CROWN LIGHT CONDITION

A detailed study of growth and crown conditions for 42 abundant tree species was conducted for stems ≥ 10 cm dbh in the lower montane forest at 1,560 m on sedimentary rock (Aiba et al., 2004, 2006). These species include four conifers (all podocarps) and 38 angiosperms. The study involved the investigation of overshadowing of each individual and its growth rate. The condition of overshadowing was expressed as a crown position index, which ranges from 1 (fully lit condition without any portion of neighboring crowns above that tree) to 4 (fully shaded by neighboring crowns above that tree). Podocarps other than *Falcatifolium falciforme* were characterized by well-lit crowns and high trunk diameter growth rates (Figure 6.8). These characteristics suggest that in this forest podocarps are light-demanding, relatively fast-growing species that require canopy gaps (e.g., by tree fall and slope failure) for regeneration and that in closed-canopy forests they are competitively inferior to angiosperms that are generally more shade tolerant. It is expected that podocarps would be eliminated from the forest in the absence of canopy disturbance.

Frequent disturbance might allow podocarps to persist in montane forest on Mount Kinabalu despite their

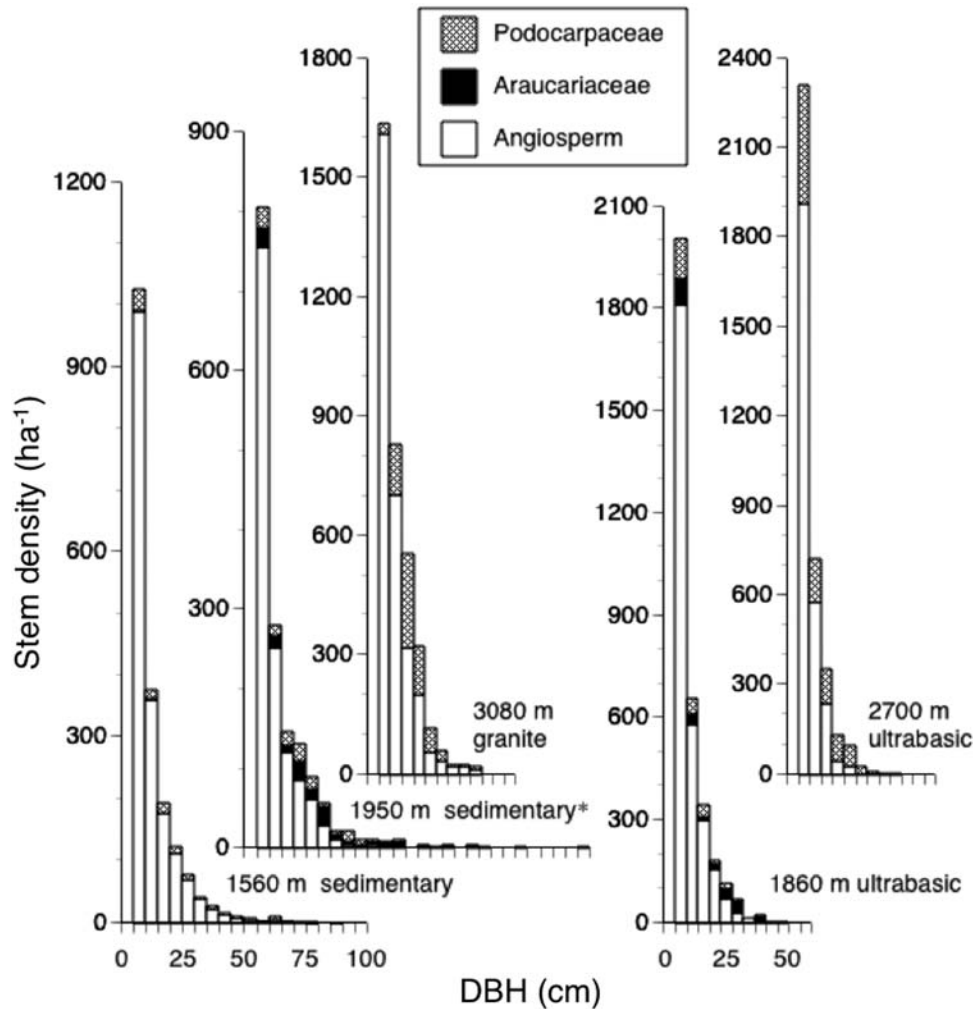


FIGURE 6.6. Diameter distribution of conifers (Podocarpaceae and Araucariaceae) and angiosperm trees in the sample plots where conifers attain dominance at various altitudes on different geological substrates. Note that the scales of the vertical axis differ among plots. The site indicated by an asterisk (*) appears to include various rock types; see footnote g of Table 6.1.

inferiority to angiosperms in shade tolerance. However, montane (and subalpine) forests are generally less dynamic than lowland forests on Mount Kinabalu in terms of population turnover rate (Aiba et al., 2005), suggesting less-frequent disturbance at higher elevations. This characteristic seems to be true even when irregular droughts associated with El Niño, which have inflated tree mortality, especially at higher elevations, are taken into account. Podocarps grow slowly because of light limitation in the forest understory. They can successfully regenerate only in well-lit conditions, but angiosperm pioneers of such genera as *Macaranga* and *Ficus* presumably outcompete podocarps on nutrient-rich soils. Only on the nutrient-deficient

soils in the montane forest where angiosperms grow slowly because of nutrient limitation can podocarps outcompete angiosperm pioneers.

ADVANTAGES AND ADAPTATIONS

In the above two sections, we described the distribution patterns, population structure, and growth rate of podocarps in the mixed evergreen conifer–broad-leaved tropical rainforests on Mount Kinabalu. Evidence suggests that podocarps have a wide temperature range (physiological niche) but are competitively inferior to co-occurring

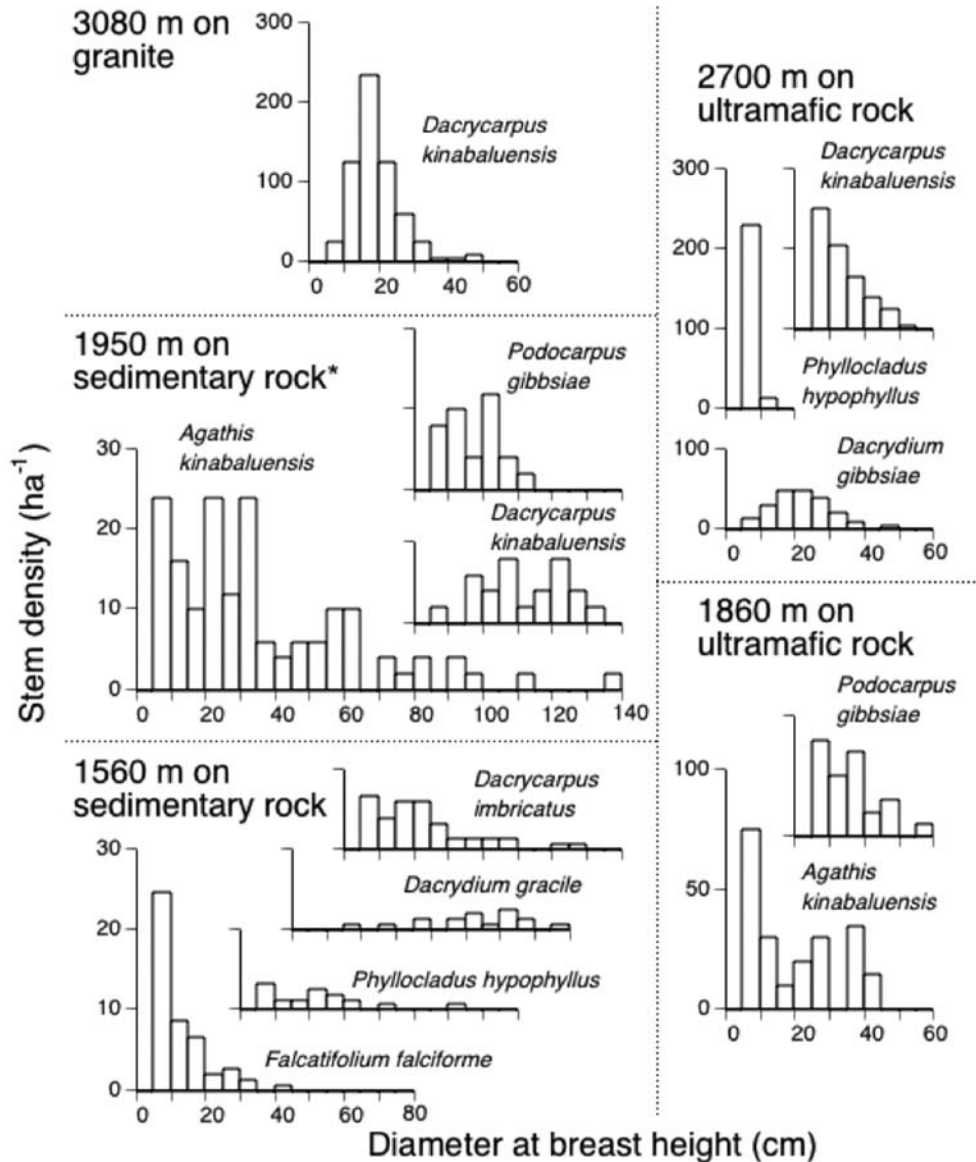


FIGURE 6.7. Diameter distribution of abundant conifers (sample size ≥ 15) in the sample plots where conifers attain dominance. All species belong to Podocarpaceae except for *Agathis kinabaluensis* (Araucariaceae). Note that the scales of the vertical axis differ among plots. The site indicated by an asterisk (*) appears to include various rock types; see footnote g of Table 6.1.

angiosperms, particularly in competition for light. It seems that when the availability of soil nutrients (nitrogen and/or phosphorus) is limited, podocarps can outcompete co-occurring angiosperms. In the following section, we discuss the architectural and life history advantages and the physiological adaptations to such nutrient limitation that allow podocarps to persist in the contemporary landscapes of the Bornean tropics.

ARCHITECTURAL AND LIFE HISTORY ADVANTAGES

Podocarps consistently form an uppermost canopy layer in the lower montane forest of Mount Kinabalu, giving an impression of their predominance. The formation of such an upper layer is not a transient process but contributes to a persistent forest structure based on their architectural traits. Figure 6.9 shows dbh–height relationships

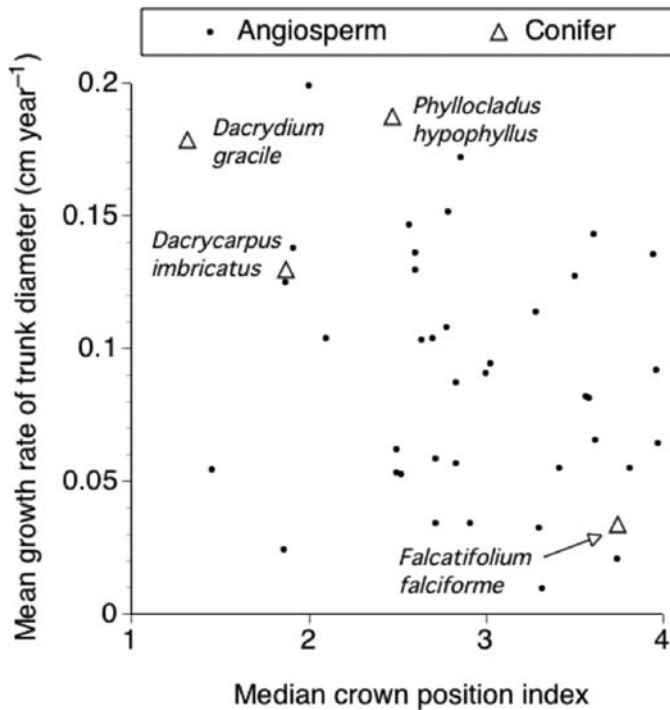


FIGURE 6.8. The relationship between median crown position index (CPI) and mean diameter growth rate at 10–40 cm diameter at breast height among 42 abundant tree species in a tropical montane forest plot at 1,560 m on sedimentary rock. Triangles indicate conifers (all Podocarpaceae), and dots indicate angiosperms. Low median CPI indicates that species are characterized by well-lit crowns in heterogeneous canopy structure. Modified from Aiba et al. (2004, 2006).

among co-occurring podocarps (*Dacrycarpus kinabaluensis*, *Dacrydium gibbsiae*, and *Phyllocladus hypophyllum*), associated *Agathis kinabaluensis*, and angiosperms in the lower montane forest at 1,950 m on “sedimentary” rock (see footnote g of Table 6.1). Two dominant conifers (*Dacrycarpus* and *Agathis*) attained a greater size in terms of both diameter and height than angiosperm trees. Moreover, when dbh–height relationships (log-transformed) were analyzed by analysis of covariance, the intercepts differed between conifers and angiosperms, and conifers were taller than angiosperm trees at a given diameter (Aiba et al., 2007). Thus, shade-intolerant conifers can survive in the forest by occupying an upper canopy layer where they can receive much sunlight.

For the above forest, we also estimated turnover time of the two dominant conifers *Dacrycarpus kinabaluensis* and *Agathis kinabaluensis* from the increase in basal area of surviving trees over nine years (2000–2009), assuming

that basal areas of individual species are in equilibrium (i.e., an increase in growth is balanced by a decrease in death if a sufficiently long period is considered). The turnover times of conifers were 168 years for *Dacrycarpus* and 364 years for *Agathis*, which were substantially longer than those of angiosperm trees (mean of 105 years for all species combined). Bornean conifers can therefore be regarded as long-lived trees that have many opportunities to regenerate during their life spans.

ACQUISITION OF PHOSPHORUS: ACID PHOSPHATASE ACTIVITY OF PODOCARP ROOTS

The soils of the tropical lower montane forests on sedimentary rock on Mount Kinabalu (where podocarps often become dominant) are broadly categorized as Spodosols, which are highly acidic (pH 3.1–4.0 in the surface horizon) and impoverished in soluble inorganic forms of phosphorus and nitrogen (Kitayama et al., 1998; Kitayama and Aiba, 2002). Kitayama et al. (2004) demonstrated that soils in the lower montane zone where podocarps were abundant were characterized by much lower total phosphorus concentrations than areas in the same zone where podocarps were rare. Further, phosphorus fractionation revealed that soil phosphorus at sites where podocarps were abundant consisted of a high proportion of physically occluded inorganic phosphate and refractory organic phosphorus, with low concentrations of labile organic phosphorus. On such soils, tree species that can acquire phosphorus from fresh litter or can scavenge labile organic phosphorus from the surface horizon may have a competitive advantage because the solubility of inorganic phosphorus fractions is extremely low. Phosphatase enzymes are required to hydrolyze phosphate from organic phosphorus in litter or soil. Phosphatases are excreted by tree roots and, in plants such as the Fagaceae, by symbiotic ectomycorrhizal fungi.

Y. Fujiki and K. Kitayama (unpublished) investigated acid phosphatase activity on roots systematically for all top to middle dominant species across three forests with differing soil phosphorus availability in the lower montane zone (1,560–1,860 m) on Mount Kinabalu. The analysis was conducted on fresh roots of seedlings of podocarps and 23 angiosperm species (Fagaceae, Myrtaceae, and other families). It should be noted that in the Fagaceae the phosphatase activity of symbiotic ectomycorrhizas is also likely to have been included in the root measurements. Roots were excavated, transported to the laboratory in a cooler box, rinsed with pure water, and assayed with *para*-nitrophenyl phosphate (a chromogenic phosphatase substrate) in acetate buffer (pH 5.0). The activity of

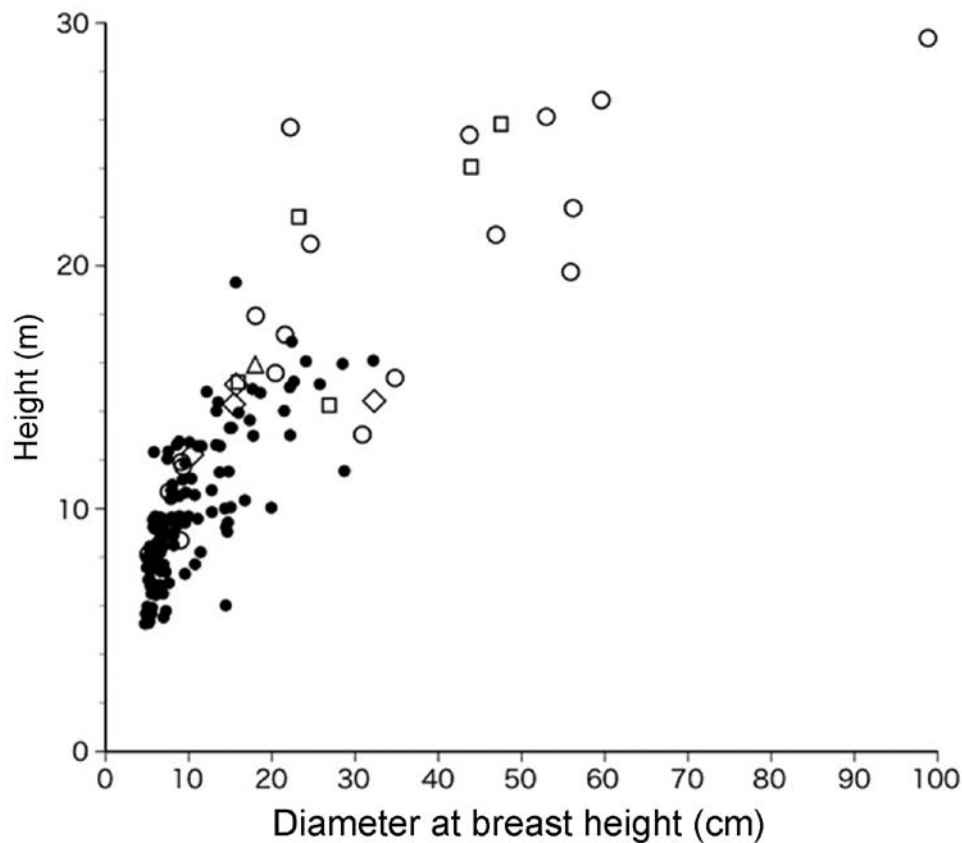


FIGURE 6.9. The relationship between diameter at breast height and tree height for conifers and angiosperms at 1,950 m on sedimentary rock (see footnote g of Table 6.1), measured in a 10×100 m transect laid in a sample plot. *Dacrycarpus kinabaluensis* (squares), *Podocarpus gibbsiae* (triangles), and *Phyllocladus hypophyllum* (diamonds) belong to Podocarpaceae, and *Agathis kinabaluensis* (circles) belongs to Araucariaceae. Black dots represent angiosperm trees.

phosphatase is expressed as the amount of product (*para*-nitrophenol) released per surface root area per unit time. The mean acid phosphatase activity on roots of Podocarpaceae (*Dacrycarpus imbricatus*, *Dacrydium gibbsiae*, *Dacrydium gracile*, *Phyllocladus hypophyllum*, and *Podocarpus gibbsiae*) was significantly greater than that of angiosperms (Figure 6.10, linear mixed model, $p = 0.03$).

The greater ability of podocarp roots to release phosphate from phosphomonoesters in organic matter may contribute to the efficient acquisition of phosphorus from litter and/or labile organic soil phosphorus fraction. This is potentially an important adaptation facilitating the persistence of podocarps on acidic montane Spodosols and is consistent with the depletion of inositol phosphate, a common phosphomonoester, as the abundance of podocarps increases in old soils along a temperate rainforest chronosequence in New Zealand (Turner et al., 2007). The same

mechanism is also advantageous on soils derived from ultramafic rocks, in which inorganic phosphate is depleted and, consequently, the contribution of organic phosphorus to plant nutrition is relatively important (Kitayama et al., 1998; Kitayama and Aiba, 2002)

SYMBIOTIC NITROGEN FIXATION

Earlier researchers speculated that podocarp roots had the ability to fix nitrogen because of the occurrence of nodule-like structures on the root surface (van Tieghem, 1870; Becking, 1965; Silvester and Bennett, 1973; Dickie and Holdaway, this volume). Roots of podocarp species (*Dacrycarpus imbricatus*, *Dacrydium gracile*, *Falcatifolium falciforme*, *Podocarpus gibbsiae*, and *Phyllocladus hypophyllum*) from the lower montane tropical rainforest at 1,560 m on sedimentary rock were assayed

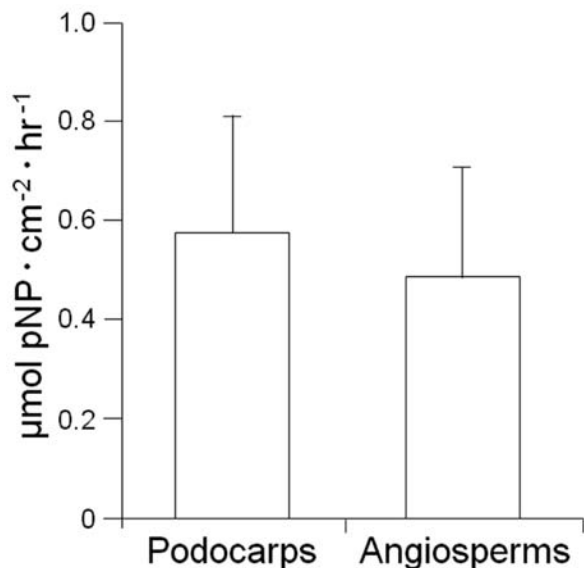


FIGURE 6.10. Mean (\pm standard deviation) acid phosphatase activity of the roots of podocarp species versus angiosperm species in the lower montane forests of Mount Kinabalu. Acid phosphatase activity is expressed as product (*para*-nitrophenol) released per root surface area per unit time. The effects of tree species taxa (i.e., podocarps versus angiosperms) on acid phosphatase activity were evaluated by a linear mixed model (acid phosphatase activity \sim taxa (podocarps or angiosperms), random effects = plant individuals).

for nitrogen-fixing ability by following the standard acetylene reduction assay of Hardy et al. (1973) (M. Ushio and K. Kitayama, unpublished). *Agathis kinabaluensis* was also included in the analysis. Significant ethylene production was not detected in all of these samples (data not shown); therefore, podocarps and *Agathis kinabaluensis* on Mount Kinabalu did not have nitrogen fixation ability (see also Dickie and Holdaway, this volume).

INFLUENCES OF PODOCARPS ON SAPROTROPHIC MICROBIAL COMMUNITIES

The abundance and composition of the soil microbial community can be affected by plant species through the chemical quality and quantity of their litter (Porazinska et al., 2003; Bartelt-Ryser et al., 2005; Kao-Kniffin and Balser, 2008). The two podocarp species (*Dacrycarpus imbricatus* and *Dacrydium gracile*) on Mount Kinabalu produce leaves in which the concentration of condensed tannins is relatively high compared to co-occurring broad-leaved species (S. Suzuki, Institute for Environmental Sciences, unpublished data). Condensed tannins can affect

the composition and abundance of the soil microbial community (Kraus et al., 2003). Therefore, it is possible that the podocarp species have impact through the effects of foliar condensed tannins on soil microbial communities, which in turn affect soil nutrient acquisition by podocarps.

Ushio et al. (2008) investigated the influences of podocarp litter on soil microbial communities in the lower montane forest on sedimentary rock at 1,560 m on Mount Kinabalu. Two podocarp species (*Dacrycarpus imbricatus* and *Dacrydium gracile*) had a distinct impact on the abundance and composition of soil microbial community (Table 6.2, Figure 6.11). Ushio et al. (2008) collected soil samples beneath five tree species (the two podocarps plus three angiosperms: *Lithocarpus clementianus*, *Palaquium rioense*, and *Tristaniopsis* sp.) that were dominant in this forest. The total lipid abundance (a proxy for microbial biomass) was greater in soils underneath *Dacrydium* than soils underneath *Tristaniopsis* ($p < 0.05$), and the abundance of specific indicator lipids also differed among some combinations of tree species (Table 6.2). The ratio of fungi to bacteria differed significantly between *Dacrycarpus* and *Lithocarpus*, between *Dacrydium* and *Lithocarpus*, and between *Dacrydium* and *Tristaniopsis* ($p < 0.05$). The ratio of Gram+ to Gram- bacteria was significantly higher in the soils underneath *Dacrydium* than in the soils underneath *Tristaniopsis* ($p < 0.05$).

A principal components analysis (the analysis of overall microbial composition) also indicated distinct species-specific effects of podocarps (Figure 6.11). *Dacrycarpus* and *Tristaniopsis* ($p < 0.05$) and *Dacrydium* and *Tristaniopsis* ($p < 0.01$) differed along PC1, whereas *Dacrycarpus* and *Lithocarpus* ($p < 0.01$) and *Dacrycarpus* and *Palaquium* ($p < 0.05$) differed along the PC2 axis. Thus, mean coordinates of *Dacrycarpus* and *Dacrydium* (both podocarp species) were not significantly different from each other, and they were different from the mean coordinates of *Tristaniopsis*, *Lithocarpus*, and *Palaquium* (angiosperms). These results suggest that the primary difference in composition of soil microbial communities exist between conifer and angiosperm species, especially in terms of the relative dominance of saprophytic fungi.

In addition to the microbial compositions, Ushio et al. (2010) investigated the activity of acid phosphatase in soils. Since plant roots were carefully removed from soil before the measurements of soil enzyme activity, the results were thought to reflect the effects of the saprophytic microbial community. They found greater activity of acid phosphatase in the soils beneath *Dacrydium* than *Lithocarpus*. They also found a significant correlation between acid phosphatase and a fungal biomarker lipid (Ushio et al.,

TABLE 6.2. Mean abundance of indicator lipids in soils beneath dominant podocarp and angiosperm tree species in a lower montane forest at 1,560 m on Mount Kinabalu. Values within rows having the same superscripted lowercase letter are not significantly different by the Tukey–Kramer honestly significant difference test (for equal variance data) or the Games–Howell test (for unequal variance data) ($p < 0.05$). Gram+ bacteria are the sum of iso-branched and saturated lipids (i14:0, 15:0, i15:0, a15:0, i16:0, 17:0, i17:0, and a17:0), actinomycetes are the sum of methyl branched lipids (17:0 10Me and 19:0 10Me), and Gram– bacteria are the sum of mono-unsaturated and cyclopropyl lipids (16:1 ω 7, cy17:0, and cy19:0). Saprophytic fungi, ectomycorrhizas/saprophytic fungi, arbuscular mycorrhizas, and protozoa are indicated by the lipid abundance of 18:2 ω 6,9, 18:1 ω 9, 16:1 ω 5, and 18:3 ω 6,9,12, respectively. The fungi : bacteria ratio is the sum of abundance of fungal lipids (18:2 ω 6,9, 18:1 ω 9) to the sum of Gram+ and Gram– lipids shown here. The Gram+ : Gram– ratio is the ratio of the sum of iso- and methyl-branched lipids to the sum of monounsaturated and cyclopropyl lipids. Values in parentheses are the standard error of the mean. Data were modified from Ushio et al. (2008).

Measurement	Lipid abundance (nmol g ⁻¹)				
	<i>Dacrycarpus</i>	<i>Dacrydium</i>	<i>Lithocarpus</i>	<i>Palaquium</i>	<i>Tristaniopsis</i>
Total lipid	1,617 ^{ab} (307)	2,309 ^a (240)	1,799 ^{ab} (336)	1,566 ^{ab} (346)	1,118 ^b (63)
Gram+ bacteria	170 (39.5)	231 (16.1)	213 (39.0)	185 (42.7)	139 (12.1)
Actinomycetes	24.1 ^a (2.7)	59.7 ^a (9.4)	52.9 ^a (13.2)	42.7 ^{ab} (16.7)	7.5 ^b (3.2)
Gram– bacteria	90.1 (15.9)	129 (6.4)	128 (22.6)	114 (21.2)	97.6 (8.7)
Saprophytic fungi	112 ^{ab} (17.0)	157 ^a (15.7)	99.5 ^{ab} (16.9)	93.9 ^{ab} (15.7)	76.6 ^b (5.9)
Ectomycorrhizas/saprophytic fungi	141 ^{ab} (30.8)	181 ^a (11.2)	144 ^{ab} (17.6)	119 ^{ab} (13.6)	101 ^b (8.9)
Arbuscular mycorrhizas	69.7 ^{ab} (13.5)	97.2 ^a (8.6)	69.9 ^{ab} (15.2)	63.8 ^{ab} (5.8)	47.5 ^b (4.2)
Protozoa	107 (19.3)	52.8 (6.3)	42.9 (19.5)	46.6 (4.7)	27.3 (5.6)
Fungi : bacteria ratio	0.99 ^{ab} (0.05)	0.93 ^b (0.04)	0.74 ^c (0.04)	0.75 ^{abc} (0.06)	0.75 ^{ac} (0.01)
Gram+ : Gram– ratio	2.11 ^{ab} (0.13)	2.28 ^a (0.17)	2.06 ^{ab} (0.17)	1.96 ^{ab} (0.17)	1.53 ^b (0.14)

2010). Therefore, the dominance of saprophytic fungi may be associated with high acid phosphatase activity in the soils beneath *Dacrydium*. However, whether the greater acid phosphatase activity feeds back to the performance of seedlings underneath a *Dacrydium* canopy is not known.

SYNTHESIS

Our review of studies conducted on Mount Kinabalu suggests that podocarps regenerate successfully primarily under well-lit conditions like canopy gaps. Fast-growing angiosperm pioneers (e.g., *Macaranga* and *Ficus* species) generally outcompete podocarps under well-lit conditions in Bornean tropical rainforests. However, such fast-growing pioneer species generally have a greater demand for nutrients (particularly nitrogen) and thus are considered inefficient in photosynthetic nitrogen use. Such nutrient-demanding pioneer species cannot grow well on nutrient-limited soils. Furthermore, the montane zone appears to be too cool for angiosperm pioneers, whereas podocarps are well adapted to a wide thermal range.

Podocarps have a greater maximum tree size than most co-occurring angiosperm species. Once they reach

the upper canopy layer, they will persist for a long time because of their longer life span, which will allow them to regenerate in rare events of canopy gap formation that are unpredictable in both space and time. Where canopy structure is sparse because of poor tree growth on extremely infertile soils derived from ultramafic rocks, however, some conifer species seem to regenerate continuously.

Our studies also suggest that podocarps (*Dacrycarpus imbricatus* and *Dacrydium gracile*) in lower montane tropical rainforest may have a superior ability over co-occurring angiosperms in acquiring phosphate from organic forms of phosphorus. This ability is consistent with the dominance of podocarps on acidic Spodosols and soils derived from ultramafic rocks; in both cases labile phosphorus occurs primarily as organic phosphorus, and consequently, the dependence of trees (as well as soil microbes) on organic phosphorus increases. Because soil phosphorus is critical in these ecosystems (Spodosols and ultramafic soils), a slight difference in the ability to acquire soil phosphorus may explain the difference in photosynthetic ability and growth rate of podocarps compared to angiosperms. Angiosperms in these systems possibly cannot outcompete podocarps under conditions where phosphorus availability limits productivity.

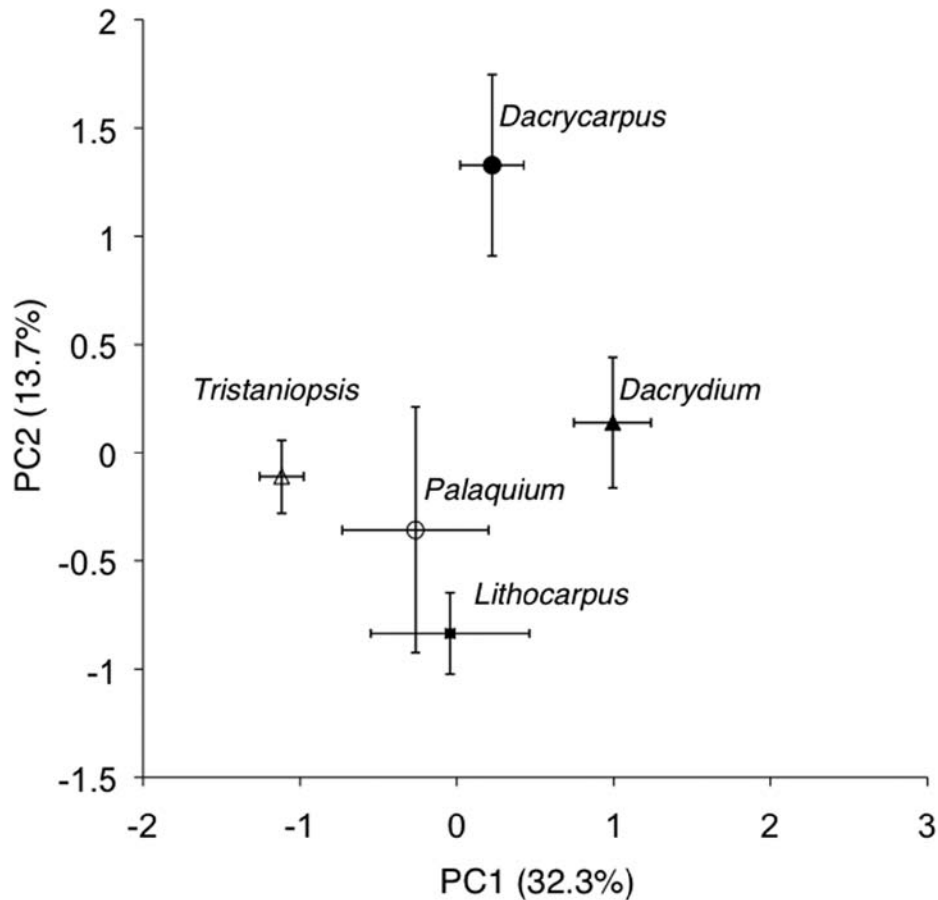


FIGURE 6.11. Principal components analysis (PCA) of soil lipids biomarkers. Lipid abundance was converted to mole percent values (each lipid abundance/total lipid abundance). The lipids with average mole percent < 0.5% were not included in the analysis. The mole percent values are not normally distributed, so the negative arcsine of the square root of each fatty acid mole percentage was used. Each point represents the mean of all soil samples for each species. *Dacrycarpus imbricatus* (solid circle) and *Dacrydium gracile* (solid triangle) are podocarps. *Lithocarpus clementianus* (solid square), *Palaquium rioense* (open circle), and *Tristaniopsis* sp. (open triangle) are angiosperms. Bars indicate the standard error of the mean and the percentages of variance explained by each axis are indicated in parentheses. Reproduced from Ushio et al. (2008).

However, phosphatase synthesis is a nitrogen-demanding process because phosphatase enzymes consist of proteins, yet we found no evidence that podocarps are superior in soil nitrogen acquisition to angiosperms. Kitayama et al. (1998, 2004) suggest that soil nitrogen mineralization is down-regulated by a decline in phosphorus availability in these systems, so soil microbes and soil nitrogen mineralization appear to be controlled by phosphorus availability. Therefore, the mechanisms of soil nitrogen acquisition must be resolved before the adaptation of podocarps to the nutrient-limited soils on Mount Kinabalu can be fully understood.

Finally, the phylogenetically associated genus *Agathis* (Araucariaceae) seems to share many traits with the podocarps. Comparison with *Agathis* would be useful to elucidate the unique ecological characteristics of podocarps in tropical forests.

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