

SECTION 3

NORWAY SPRUCE (*PICEA ABIES* (L.) KARST)

1. General Description and Use in Forestry

A. Taxonomy

Norway spruce (*Picea abies* (L.) Karst) belongs to the genus *Picea*, which includes at least 36 different species that all have their distribution in the northern hemisphere (Schmidt-Vogt 1977). The species *P. abies* has been designated by a large number of synonyms, partly caused by classification to different species or subspecies due to its great number of varieties and forms. The best known of these is the classification of the Siberian spruce in a separate species, *P. obovata*, based on the shape of its cone scales. These variations, however, should be considered as normal patterns of variation within a widespread species and should at most be used to designate different climatic varieties (Schmidt-Vogt 1977, 1978).

B. Use of Norway spruce

Norway spruce is the economically most important conifer tree species in Europe. It has a long history of cultivation in central Europe, and has been seeded and planted very intensely since the middle of the 19th century. This has changed natural forests into artificial ones and has led to the species' introduction far outside its natural range, both in countries where it occurs naturally (*e.g.* Germany and Norway) and in new countries such as Denmark, Belgium and Ireland. To some extent, Norway spruce has also been planted in North America.

Norway spruce has shown good yield and quality performance under very different site conditions, and this favoured the species over a long period. In some areas, where maladapted provenances were used, damage and reduced yield have occurred. In the last two decades the species has suffered severely during the forest decline in central Europe, resulting in stands with high percentages of trees with needle loss (Wolf 1995) or in completely destroyed stands (Vancura 1995). The health problems of the central European spruce forest, and reduced possibilities for recreation in young spruce stands, have to some extent reduced the popularity of this species for reforestation, particularly outside its natural range.

2. Forest Practices for Norway Spruce

A. Breeding of Norway spruce

Usually the goal of breeding programmes is to produce superior material for reforestation by managing genetic variability. Breeding of Norway spruce was initiated in several European countries in the late 1940s (Danell 1991, Mikola 1993). In some countries the work started with the selection of phenotypically superior trees ("plus trees") in natural stands (Skrøppa 1982b, Mikola 1993, Gabrilavicius and Pliura 1993). Mature trees that had superior height and diameter growth, and stem and branch quality, compared to neighbouring trees in the stand were selected. They were grafted in multiple copies on rootstocks in clonal archives or seed orchards. Each grafted seed orchard is composed of a rather large number of selected clones (50-500), with the intention of seed production for one geographic region. The

seed orchard will generally start to flower 10-15 years after grafting. However, both the regularity and amount of flowering are very dependent on climatic conditions at the orchard site. To promote flowering, seed orchards have often been located to sites with a warmer climate than that from which the selected parents originate and where the orchard seed is intended for use.

It was soon realised that the selection of plus trees in natural Norway spruce stands is not an efficient method of selecting superior genotypes. It is necessary to test the genetic value of each parent, based on an evaluation of its offspring. In Norway this is done in progeny tests planted at several sites, where measurements are made of survival, height and diameter growth, and quality traits. The progeny tests are sometimes supplemented with tests in which seedlings are grown under controlled conditions in growth chambers and measurements are made of physiological traits. On the basis of several traits, a subset of the original parents is selected for further breeding. Seeds for practical planting can be collected in the orchard from the selected parents, the orchard can be thinned, or a new orchard can be established based on the selected group.

In other countries, breeding programmes were based on selected materials from populations with high adaptive potentials observed in comparative provenance trials. According to performances measured in progeny trials with families from these populations, the best individuals within progeny were selected either directly to produce seeds in seed orchards, or to create a breeding population through controlled crosses. Some of these programmes were also aimed at mass production of rooted cuttings of tested and selected clones (Biro 1982, van de Sype and Roman-Amat 1989, Kleinschmit 1993). Of major concern in the development of breeding strategies have been the breeding objectives; the sizes of the breeding and seed producing populations required to maintain genetic diversity; design and efficiency in testing; and identification of suitable regions where the orchard seed should be recommended for use. Based on test results, gains from the original plus tree selection have been estimated, at 6% genetic improvement in height growth at stand closure (Danell 1991). An additional 10% advance in the selected trait can be expected after progeny testing and further selection.

In Norway, Sweden and Finland several thousand selected spruce trees have been grafted in seed orchards or clonal archives. A large number of these have been progeny tested. Most seed orchards, however, consist of the original set of non-tested parents. In some orchards selective harvests have been made on the basis of progeny test results. The main selection criteria have been traits characterising the annual growth rhythm, height growth, and the avoidance of damage in field tests. Artificial freezing tests are being used to determine autumn frost hardiness, particularly for materials intended to be planted at high altitudes or far north. Each seed orchard is intended to produce seed for a specific region, which is determined by the origin of the parents and the growth rhythm and hardiness performance of the orchard offspring.

Seed orchard breeding is also the most common technique being used for spruce in central and eastern Europe (*e.g.* Dolgolikov 1993, Gabrilavicius and Pliura 1993, Kleinschmit 1993). Special types of orchards have been established, based on materials from provenance trials, in order to reconstitute provenances that probably no longer exist or are untraceable (Giertych 1993). Clonal breeding programmes based on rooted cuttings have been developed in Germany (Kleinschmit 1993) and Sweden (Karlsson 1993).

B. Reproductive methods

Flower induction

Application of growth regulators, primarily gibberellins, has become an efficient method of regulating flowering in forest trees. In the case of Norway spruce grafts, treatments during the shoot growth period (with gibberellic acid alone and in combination with heat) have been efficient in promoting female

flowering (Johnsen *et al.* 1994). Heat treatment alone will induce male flowering. Of mechanical flower stimulation techniques attempted in Norway spruce seed orchards, only thinning is useful on a larger scale (Schneck *et al.* 1995). The problem of shortening the juvenile phase and obtaining regular flowering at an early age remains unsolved (Chalupka 1991).

Vegetative propagation

Norway spruce has for decades been propagated by grafting. Scions to be grafted are taken from the crown of mature trees and grafted onto a rootstock, which is a young spruce seedling. This technique is being used to establish clonal seed orchards and clonal archives.

Vegetative propagation with rooted cuttings is easily achieved with young spruce seedlings and can be applied on a large scale (Kleinschmit *et al.* 1973). The propagation can be made either in early spring before bud flushing, or after shoot growth terminates at the end of the summer. Both the rooting capacity and the growth form of the cutting depend on the age of the cutting donor, but they can be improved in a proper rooting environment. A large genetic variation has been observed in rooting capacity and subsequent growth habit of the cutting (Johnsen and Skrøppa 1992). Several systems of propagation have been developed in order to keep the plant material at a juvenile stage (Roulund 1981, Dekker-Robertson and Kleinschmit 1991). Clonal tests with rooted cuttings have provided valuable information for Norway spruce genetics research, in addition to providing clonal material with high genetic value intended for commercial use (*e.g.* van de Sype 1989, Kleinschmit and Svolba 1991, Isik *et al.* 1995).

Cell and tissue culture techniques for micropropagation have recently been developed for conifers. The most promising method for Norway spruce appears to be somatic embryogenesis, obtained for the first time by Hakman *et al.* (1985). Somatic cells are stimulated to develop into somatic embryos, somewhat analogous to that of a zygotic embryo. The somatic embryo can be stimulated to mature and develop into a plant which will be of the same genotype as the zygotic embryo used for induction of this embryogenic cell line (Hakman 1993, von Arnold *et al.* 1995, von Arnold 1996, Egersdotter and von Arnold 1998). However, in *P. abies* somatic embryogenesis has also been initiated from explants other than zygotic embryos (Wescott 1994, Ruaud 1993). The somatic embryos can be propagated in unlimited numbers on a large scale and can be formed as artificial seeds. The method works only for a limited number of genotypes and requires controlling plant quality. Therefore, further developments are needed before somatic embryogenesis can be used for practical forestry purposes (Mo 1993). Norway spruce also belongs to the few spruce species with advanced *in vitro* regeneration, and thus could have possibilities for genetic transformation. There has recently been a breakthrough in production of stably transformed Norway spruce, based on *Agrobacterium tumefaciens* mediated transformation (Wenck *et al.* 1997) and on biolistic transformation (Walter *et al.* 1997). Also, genetic transformation of Norway spruce pollen and the use of transformed pollen in controlled pollinations is in progress (Häggman *et al.* 1997).

C. Reproductive materials used

The regeneration of Norway spruce forests is based on both natural regeneration and planting, with an emphasis in many countries on natural regeneration where that is a feasible method. The largest proportion of Norway spruce seeds being used world-wide are collected in natural or planted stands. Each seed lot is identified by the geographic origin of the stand. In several countries it is required that the seed stand be selected for superior performance (EEC 1966, Muhs 1986). The relative amounts of stand and seed orchard seed being used vary considerably between countries, and between regions within countries. Clonal forestry based on rooted cuttings, which was initiated to some extent in the 1970s in Germany and Sweden, occurs at present only on a small scale.

In the Nordic countries, stand seed accounts for the largest proportion of seed used. The percentages of stand seed used in 1994 were: 89% (Denmark), 84% (Sweden), 81% (Norway) and 80% (Finland) (personal communication Bjerne Ditlefsen, Lennart Ackzell, Gunnar Haug, Hannu Kukkonen). The percentage from seed orchards varied between 10 and 20%. Sweden is the greatest importer of spruce seed, 35% of which is stand seed. Rooted cuttings account for less than 1% of the total number of Norway spruce plants.

D. Provenance transfers

The first provenance transfers were more or less random and unrecorded, with the result that in large areas of central Europe and southern Scandinavia most spruce stands are of unknown and mixed origins. Subsequently, provenance trials have provided information about the effects of transferring provenances from different parts of the range of the species and have identified provenance areas which generally have both a high adaptability potential and high growth capacity. Examples are provenances from southern Poland and Romania, which have been planted with success in several countries (Lacaze 1969, Krutzsch 1992, van de Sype 1998). Some other provenances present a low adaptation potential and exhibit huge variations in performance for survival rate and growth ability according to trial location (*e.g.* van de Sype 1998).

Provenance transfers have been used deliberately in several cases where materials with specific adaptive properties were sought. An example is the transfer of late-flushing Norway spruce provenances from Byelorussia and the Baltic countries to sites exposed to late spring frosts in southern Sweden. These provenance transfers have reduced frost damage and improved growth (Werner *et al.* 1991, Werner and Danell 1993). In other cases, however, maladaptation has occurred, particularly after transfers of provenances from a warm to a colder climate. In south-eastern Norway, spruce provenances from Austria and southern Germany were extensively planted during a 20-year period starting in the 1950s. A survey of 79 planted stands of central European origin and 21 of local origin, all at the age of 27 years, was recently made in Østfold County, Norway (Skrøppa *et al.* 1993). In the stands of local origin, 30% of trees were classified as having saw timber qualities, while only 7% of those in the central European stands obtained the same quality classification. This provenance transfer generally had a negative effect on timber quality and a small positive effect on volume production, even if a few of the stands planted with southern provenances had both high volume production and good stem quality. It is not known to what extent the pollen cloud from these stands may cause reduced fitness in offspring from the seed in neighbouring stands of local origin.

E. Conservation of Norway spruce genetic resources

In many countries the combination of natural regeneration and planting of materials with a broad genetic diversity is the basis for conservation of genetic resources of Norway spruce. In addition, several specific conservation measures are taken. *In situ* activities include national parks, nature reserves and specific conservation or gene reserve forests. The grafted clone banks and seed orchards and provenance and progeny tests constitute the *ex situ* gene conservation, together with long-term seed storage. Co-operation at the European level is achieved through the recently established European Forest Genetic Resources Programme (EUFORGEN). Norway spruce is one of the species for which a co-operative network has been formed (Turok *et al.* 1995, Turok and Koski 1997, Koski *et al.* 1997).

3. Centres of Origin and Immigration History

A. Natural distribution and origin

The natural distribution of *P. abies* can, according to Schmidt-Vogt (1977), be divided into three areas: the central and south-eastern European, north-eastern European and Siberian spruce areas. The first covers mainly mountainous and sub-alpine regions and is separated from the second by a spruceless area in Poland. The north-eastern European area includes the Baltic, Nordic and Russian spruce. The Siberian area covers all spruce east of the Urals.

The total natural distribution of *P. abies* covers 31 degrees of latitude from the Balkan Peninsula (latitude 41°27'N) to its northernmost extension near the Chatanga River, Siberia (latitude 72°15'N). Longitudinal range is from 5°27'E in the French Alps to 154°E at the Sea of Okhotsk in Eastern Siberia. The vertical distribution is from sea level to altitudes above 2 300 m in the Italian Alps. Outside this area the species has been widely planted, particularly in central Europe (Ellenberg 1988) and in Scandinavia.

It is thought likely that *P. abies* had its prehistoric origin in east Asia, from which it migrated to Europe through Siberia and the Urals (Schmidt-Vogt 1977). During the last Ice Age, the species is assumed to have survived in refugia in four European regions: north-central Russia, the Carpathians and Transylvanian Alps, the Dinaric Alps and the Apennine peninsula. From these refugia, *P. abies* migrated to its present natural areas. The central and south-eastern European spruce originate from the last three refugia, while the north-eastern European spruce migrated from Russia.

In central Europe, *P. abies* could probably be found only in two small areas in the present Czech Republic about 11,500 BC (Vancura 1995). It migrated from the Beskids over the Sudeten to the Ore Mountains in Germany, which were reached about 6500 BC. Spruce established in the Harz Mountains about 4000 BC, while the Black Forest in south-western Germany was reached about 1500 BC. In Switzerland, Norway spruce established in the eastern and south-eastern part of the country about 8000 years ago and expanded to the valleys of the Alps within 3500 years (Bonfils and Sperisen 1997). The expansion was much slower North of the Alps.

The migration of Norway spruce to Fennoscandia took place from the Russian refugium. It advanced through the forest area at the present border between Russia and Finland and passed through Finland and northern Sweden into Norway in the period 3500-500 BC (Moe 1970, Schmidt-Vogt 1977, Hafsten 1991, 1992a, b). The advance was quite rapid; it has been estimated at an average speed of 9 km every ten years (Moe 1970).

4. Reproductive Biology

A. Sexual reproduction

P. abies is monoecious, having both male and female flowers on the same individuals but on separate organs. The male flowers are in most cases located at the base of the preceding year's shoot, while the female strobili are at the tip of the shoot, directed upwards. The reproductive buds are initiated during the growth season the year before.

Male meiosis and pollen development occur after the winter dormancy in late winter or early spring and are regulated by the temperature conditions (Luomajoki 1993). A male flower may contain as many as 600 000 pollen grains, which are released at anthesis and dispersed by wind.

Female meiosis usually starts before the female strobili become receptive (Sarvas 1968) and occurs close to or during the period of pollination. Pollen grains are accommodated in a pollen chamber which has

a limited volume and, on average, contains three to five pollen grains. They germinate and pollen tubes grow towards the female gametophyte (egg cell) in the ovule, where fusion of the male and female gametes takes place. Under natural conditions this normally occurs five to six weeks after pollination. The fertilised egg develops rapidly into a seed. Several egg cells may be fertilised in each ovule, but only one will develop into a seed. Empty seeds may result from lack of pollination or from abortion.

Climatic conditions play an important role during several stages of the reproductive process. High temperature during the growth season is one of the main factors favouring floral initiation and the development of reproductive buds which will flower the next spring. Dry conditions and moderate to high temperatures during the flowering period the following year are necessary in order to obtain sufficient pollination. Seed development and maturation require high accumulated temperature sums during the summer and early autumn. Such specific weather patterns during two successive years occur rather seldom, particularly far north and at high latitude regions, which may explain why seed crops are both rare and irregular in these areas.

B. Mating system and gene flow

The mating system of Norway spruce falls into the mixed mating category. That is, the largest part of the seeds are produced through cross-fertilisation and the rest through self-fertilisation. Cross-fertilisations are both between trees that are close together in a stand, and among distant individuals in the same or nearby stands.

Spruce pollen is able to move over long distances. Andersson (1955) found that the amount of pollen at 2 500 m distance was 47% of the amount at the edge of the forest in one stand, and 15% in another stand. In two Norway spruce stands in Finland, Koski (1970) estimated the background pollination to be approximately 60% of the total pollen catch. Lindgren *et al.* (1991) reported results from studies of the dispersion of Norway spruce pollen artificially released in seed orchards outside the local pollen shedding season. These results showed a rapid drop-off in the pollen dispersion curve over distance from the source, with the largest amount of pollen being deposited less than 50 meters from the pollen source. However, large variation patterns most likely due to wind turbulence were found between pollen catches on individual days, indicating that a curve showing a smooth movement in the wind direction is not a good model for individual pollen dispersion events (Lindgren *et al.* 1991).

Both local and long-range pollen movements will determine the natural pollination patterns and actual gene flow of Norway spruce. On average, most pollinations will be with local pollen or pollen from nearby populations (Koski 1970), with exceptions in some years. In an allozyme marker genetic study in an experimental Norway spruce plantation, Xie and Knowles (1994) estimated the proportion of ovules fertilised with own pollen, pollen from trees within the plantation and that from trees outside the plantation to be 0.09, 0.75 and 0.16, respectively. The proportions varied considerably among parent trees. Wind-pollinated forest trees are known to have a high number of migrants per generation compared to other plant species (Govindaraju 1988, 1989). No good estimates of migration rates are available for Norway spruce, but Koski (1970) and Finkelday (1995) both concluded that the gene flow between nearby populations by means of pollen dispersal is effective and may play an essential role in the population genetics structure of Norway spruce.

The actual rate of self-fertilisations in natural populations may vary considerably between trees. It was found by Müller (1977) to vary between 7 and 18% in a study of five trees. Koski (1973) estimated the mean proportion of self-fertilisations at 10%, but concluded that only 1% of the filled seeds originate from self-fertilisations.

C. Inbreeding depression

Most spruce trees will produce some filled seed after self-pollinations, but the seed yield is much reduced (Skrøppa and Tho 1990). The main reason for this is embryo abortions caused by lethal or deleterious genes that become harmful when they occur as recessive homozygotes in the selfed individuals (Koski 1971). Inbred spruce trees generally have reduced fitness compared to their outbred relatives. They have lower survival in the field, their growing season is shorter, and they grow more slowly (Langlet 1940, Eriksson *et al.* 1973, Skrøppa 1996). The inbreeding depression varies both among populations and among individuals within the same population (Skrøppa 1996). For a trait such as height growth at age ten years, it may vary in the range of 10 to 50% among selfed offspring of trees from the same population.

D. The seed crop

Norway spruce trees undergo a rather long juvenile period, during which they will not flower and set seeds. In the open stand, sexual maturity will generally be reached after 20-30 years, while it occurs later in the closed stand (Schmidt-Vogt 1978). However, a substantial flowering and seed set may occur considerably earlier than 20 years from planting (Skrøppa, unpublished) if the temperature conditions are favourable for floral induction. In exceptional years, female flowering has been observed on eight- to ten-year-old and male flowering on twelve- to 15-year-old Norway spruce trees.

Under central European conditions, Norway spruce will flower several times in a decade (Schmidt-Vogt 1978). In the boreal forest, cone harvests occur less frequently and at irregular intervals. There were no cone crops in the lowlands of southern Norway between 1976 and 1983. Since then, however, substantial flowering and seed crops have occurred in 1983, 1987, 1989, 1993 and 1995. In northern Norway, successful seed harvests have been obtained only three times during the last 40 years (1958, 1970 and 1981).

In central European seed orchards, flowering has occurred less frequently than was expected (Kleinschmit 1993).

E. Natural regeneration

The Norway spruce seeds are dispersed mainly by wind and partly by birds and animals (Sokolov *et al.* 1977). Most seeds will be dispersed close to the mother tree, but some may also be dispersed over larger distances.

Natural regeneration also very much depends on the species composition of the bottom and field layer. The most productive spruce forest appears to be the most problematic for natural regeneration, for example in “spruce forest with tall herbs” (*Melico-Piceetum aconitosum*) and “spruce forest with tall ferns” (*Eu-Piceetum athyrietosum*). The optimal habitat for natural regeneration is the “spruce forest with small ferns” (*Eu-Piceetum dryopteridetosum*). Regeneration in our most common and widespread spruce community, “spruce forest with bilberry” (*Eu-Piceetum myrtilletosum*), is greatly hampered by a thick raw humus layer, especially at higher altitudes (Mork 1944, 1945, 1968).

The Norway spruce seedlings are very shade-tolerant and can survive for decades under a closed canopy (Siren 1955). They grow slowly during the first years, and the height growth increases after five to ten years (Sokolov *et al.* 1977, Nikolov and Helmisaari 1992). *P. abies* is often associated with grey alder (*Alnus incana*) on river plains in the boreal zone and may tolerate occasional flooding (Sokolov *et al.* 1977).

F. Dynamics of regeneration

Boreal forests undisturbed by human activity have dynamic properties, with complex succession stages which influence habitats and create possibilities for regeneration. The most important natural disturbance factors are fire, storms, and pathogens such as bark beetles (Tømmerås 1994). The fire tolerance of *P. abies* is very poor (Drakenberg 1981). Mainly due to its shallow root system, spruce is intolerant to windthrow (Sokolov *et al.* 1977). Storms can blow down many trees, particularly in wind-exposed areas, where occasionally almost all the trees in a stand may blow down. Bark beetles (*Ips typographus*) can from time to time become a serious pest and kill trees (Christiansen and Bakke 1988). Together with gaps created by the death of individual old trees, these disturbances open up the canopy and lay the foundation for regeneration.

G. Vegetative reproduction in nature

Under certain conditions, Norway spruce will naturally reproduce vegetatively through the lowest branches, which may come into contact with the soil and differentiate roots and new shoots (layering). This occurs particularly in alpine areas, where the climatic conditions prohibit sexual reproduction, and is therefore important for species distribution (Skoklefeldt 1993). Examples of such vegetative reproduction can be seen above the timberline where scattered clonal groups occur.

5. Crosses

A. Crossability with other species

Crossability of spruce species can be judged both from introgressive hybridisation and from attempted controlled hybridisation. The only known natural hybrids involving Norway spruce are *P. abies* var. *obovata* with *P. jezoensis* and *P. koraiensis* (Schmidt-Vogt 1977) in eastern Asia. Successful artificial hybridisations are reported with eight other spruce species (*P. asperata*, *P. glauca*, *P. mariana*, *P. montigena*, *P. omorica*, *P. orientalis*, *P. rubens* and *P. sitchensis*) (Kleinschmit 1979). Rather few of the potential hybrid crossing combinations have been attempted.

B. Interprovenance hybridisation

No crossing barriers are present between spruce trees from different provenances. Provenance hybrids are therefore produced naturally in regions with both indigenous populations and introduced provenances or cultivars. The extent and implications of these hybridisations depend on many factors, such as the characteristics of the provenances discussed in section VI.

Experimental results with inter- and intraprovenance crosses have demonstrated that the hybrids are intermediate between the two parents for most traits (*e.g.* Ekberg *et al.* 1982, 1991, Kaya and Lindgren 1992). Hybrid vigour therefore does not appear to be present to any large extent.

6. Genetic Variability

The number of chromosomes of Norway spruce is $2n = 24$ (Schmidt-Vogt 1977 and references cited therein). Tetraploidy has occasionally been observed in Swedish and German provenances (Kiellander 1950) and has also been induced by colchicine treatments (Johnsson 1975). Trees with irregular chromosome numbers appear in general to have reduced fitness.

The genetic variability of Norway spruce has been studied using a large number of methods and at different genetic levels. More than 100 years ago, experiments replicated at several locations with seed lots from different origins (provenances) were carried out in Austria, Germany and Switzerland (Langlet 1971).

In these first genecological experiments, traits such as height increment, needle morphology, growth habit, time of growth initiation and frost damage were studied. Later, both national and international provenance experiments were established, some of these organised by the International Union of Forest Research Organisations (IUFRO), and often including large numbers of provenances planted on multiple test sites in several countries (Krutzsch 1992). The traits studied are related, in particular, to forestry cultivation of Norway spruce. They characterise climatic adaptation, growth potential and quality. They are typically quantitative, having a continuous phenotypic distribution, and are strongly influenced by the environment. The same type of traits have been measured in numerous experiments with offspring from both natural and artificial populations, in most cases established with the intention of testing breeding materials. The field trials have been supplemented by tests under more controlled conditions, in which variability in specific physiological traits has been studied. Since biochemical markers became available, several population genetics studies have characterised the intra- and interpopulation variation and genetic structure of the species (*e.g.* Lagercrantz and Ryman 1990, Müller-Starck *et al.* 1992, Konnert and Maurer 1995). Recently, molecular DNA marker techniques have been developed for Norway spruce (Bucci and Menozzi 1993, Binelli and Bucci 1994).

A. Overall variability

Large genetic variability exists within the extensive range of the natural distribution of Norway spruce. The most pronounced adaptive patterns relate to populations' responses to climatic conditions. Across the European range of the species these patterns of variability can often be related to latitude and altitude of origin, and with degree of continentality, and will sometimes vary clinally. In central Europe, however, differences among populations from the same geographic region are in many cases large and reflect several generations of Norway spruce cultivation. This fact often blurs patterns of variation of adaptive traits. Traits that characterise the annual growth cycle, particularly onset of growth in the spring and termination of growth and development of frost hardiness in late summer, show the most pronounced provenance variability (Langlet 1960, Krutzsch 1975, Dormling 1973, Beuker 1994, Beuker *et al.* 1998). However, observations of these and of growth performance traits are made in common garden field tests comparing provenances that are transferred unequal distances. Such provenance transfers may affect provenances differently. Provenance differences must therefore always be interpreted relative to the planting site conditions.

Populations with an early growth start, often expressed as bud burst or bud flushing, originate from high latitudes in northern Scandinavia, Finland and Siberia and from high altitudes in the central European Alps (Langlet 1960, Krutzsch 1975, Holzer 1993, Beuker 1994). The eastern and more continental provenances generally have a late growth start, and the latest flushing populations come from Byelorussia, north-eastern Poland and the interior of the Baltic Republics. The variation in bud flushing and initiation of shoot growth of Norway spruce provenances are assumed to be regulated both by differential responses to accumulated temperature sums in the spring and by conditions during acclimation the preceding year (Heide 1974b, Schmidt-Vogt 1977, Dormling 1982).

Photoperiod is the environmental factor that initiates the cessation of growth and development of frost hardiness (Dormling 1973), but with some modifications caused by temperature (Heide 1974a). Under controlled growing conditions in growth chambers, seedlings of provenances from the northernmost latitudes will respond with a terminal bud set at a night length of two to three hours, compared to eight to nine hours of darkness for south-western European origins (Dormling 1973). The northern Scandinavian and Finnish provenances, and those from high altitudes in the Alps, have the earliest cessation of shoot growth (Skrøppa and Magnussen 1993). The latest growth cessation occurs in provenances from southern Poland and the eastern Carpathians.

At the provenance level, strong relationships are generally present between traits that characterise the timing and duration of the growth period, the lignification of the annual ring, and the development of autumn frost hardiness (Skrøppa and Magnussen 1993, Ekberg *et al.* 1994). These traits are components of an annual sequence of developmental events which describe the inherent annual rhythm of trees of the same provenance (Sarvas 1972, Skrøppa and Magnussen 1993).

Resistance to late spring frost is closely related to the time of growth start; the late flushing provenances from eastern Europe suffer less damage than native Nordic provenances during spring frost events in Scandinavia (Werner *et al.* 1991). A similar but somewhat weaker relationship is present between the timing of growth cessation and resistance to autumn frost. Provenances with early termination growth will normally enter dormancy (develop frost hardiness) earlier than those extending their growth period late in the summer, and thus be less damaged by early autumn frosts. In the Alps, high altitude provenances will be more resistant to early autumn frosts than those of lowland origins (Holzer 1993).

The growth capacity of different provenances is closely related to the duration of their growth period (Holzer 1993, Skrøppa and Magnussen 1993). Northern provenances, or those from high altitudes that are adapted to a short growth season, will therefore have a poorer growth potential than those adapted to a longer season. Two provenance regions with particularly high growth potential have been identified (Schmidt-Vogt 1978). One covers parts of the post-glacial advance of spruce from the Russian refugium, including the Baltic Republics, north-eastern Poland and northern parts of Byelorussia. The other region covers the eastern Carpathian and Bihor Mountains and parts of the Beskids.

Wood quality traits, such as basic wood density and its determining components, have been shown to vary considerably among different provenances (Mergen *et al.* 1964, Worrall 1970, Schmidt-Vogt 1986). They are also influenced by the extent of provenance transfer. Strong relationships exist between these traits and annual growth rhythm characteristics.

Provenance variation has been shown for a number of other traits, such as nutrient demands, respiration activity and shade tolerance (Schmidt-Vogt 1977). Provenance differences are present in crown form, related to snow and ice break resistance, with the resistance increasing according to altitude (Holzer 1964, Schmidt-Vogt 1977).

Enzyme genetic marker studies reveal a great genetic variability within Norway spruce populations (Müller-Starck *et al.* 1992, Goncharenko *et al.* 1995), and also in populations close to the climatic margin of the species (Tigerstedt 1973, 1979). In the most comprehensive isozyme study on Norway spruce (Lagercrantz and Ryman 1990), only 5% of the total genetic diversity was explained by differences among provenances. Some differentiation occurs among populations derived from different glacial refugia and appear to reflect their post-glacial evolutionary history (Lagercrantz and Ryman 1990). Populations from the same region show little genetic differentiation (Bergmann 1973, Lundkvist and Rudin 1977, Lundkvist 1979, Konnert and Franke 1991). Central European provenances appear to have reduced genetic diversity, expressed by a reduced level of average heterozygosity compared to those from eastern Europe and Scandinavia (Lagercrantz and Ryman 1990, Goncharenko *et al.* 1995).

Patterns of provenance variation show geographic variability on a large scale. However, genetic variation may be present between offspring from populations within the same provenance, and this variation is often larger than that between provenances. Dietrichson (1973) sampled three populations from the same altitude (620-750 m) in each of five provenances, covering an area of 200 km north-south and 250 km west-east in southern Norway. Measurements were made of heights at two and four years, growth initiation and cessation, and lignification of the annual ring. Several traits showed a larger variation among populations within a provenance than among provenances. In studies of clones sampled from several populations from the same provenance region and from different provenances, variation among clones has

been demonstrated for a large number of traits (Sauer *et al.* 1973, Sauer-Stegmann *et al.* 1978, Kleinschmit *et al.* 1981, 1981).

B. Variability within populations

The large within-population genetic variation demonstrated by genetic markers has been confirmed in studies of quantitative traits. Genetic variability has been found within all natural Norway spruce populations studied, as well as for traits that show clinal variation at the provenance level (Dietrichson 1971, 1973, Eriksson 1982, Skrøppa 1982a, Ekberg *et al.* 1985, 1991). Traits that show such variation characterise germination, early and later height and diameter growth, the timing and duration of the shoot growth period, autumn frost hardiness, survival in the field, and branch, crown form, stem and wood quality (Schmidt-Vogt 1977, Skrøppa 1991, 1993, Hylén 1997). The range of variation may sometimes be as large as that found between geographically distant provenances.

C. Resistance to fungi and insects

Studies investigating Norway spruce's resistance to root rot (*Heterobasidion annosum*) have been carried out at both the provenance and clonal level (Dimitri and Kliefoth 1980). Treschow (1958) found no variation in growth of *H. annosum* among trees of different provenances. In an inoculation experiment with *H. annosum* on 98 Norway spruce clones, differences among clones were found in lesion length and fungal growth in sapwood (Swedjemark and Stenlid 1996). This indicates the presence of genetic variation among individual clones in degree of resistance to the fungus, and indicates that progress in resistance can be achieved through selection. Similar variation among clones has been found in resistance to bark beetle fungus infection (*Ceratocystis polonica*) (Christiansen and Berryman 1995, Brignolas *et al.* 1995).

Differences have been demonstrated among provenances in respect to infestation by spruce aphids (*Adelges* ssp.) (Balut and Sabor 1993), and also among families and clones from the same population (Skrøppa, unpublished). Little information is available on genetic variation in resistance to attacks by other insect species.

D. Factors influencing the genetic variability

The great genetic variability of the Norway spruce forests is influenced by a large number of factors: ancient origin and immigration history, natural selection, an extensive gene flow caused by pollen dispersal, genetic drift due to small population size, and human activities.

Different factors may cause specific variation patterns to be present in parts of the range of the species. As an example, in some areas the existence of frost pockets or different slopes and exposure aspects may have resulted in selection of different annual growth rhythms. Patterns of spacial differentiation may therefore be the result of complex interactions of gene flow and selection (Finkelday 1995, Krutovskii and Bergmann 1995). In central Europe the species has been cultivated for more than 300 years, partly with seed material transferred from other regions. Differences in performance between provenances from the same region therefore may not exclusively express adaptational differences. Recent experimental results indicate that phenotypic provenance variation in traits characterising climatic adaptation is not only regulated by classical (Mendelian) gene frequency differences, but also by other mechanisms (*e.g.* gene regulation). These mechanisms appear to be triggered by environmental influences during the generative reproductive process (Skrøppa and Johnsen 1994, Johnsen and Skrøppa 1996, Johnsen *et al.* 1995, 1996).

7. Ecology

A. Synecology and associated species

Spruce forests are found in many different habitats. They usually belong to the acidophilous order *Vaccinio-Piceetalia* and to a lesser extent to the *Fagetalia* (Ellenberg 1988, Fremstad 1997).

Forests of *P. abies* play a dominating role in the boreal zone in Fennoscandia and northern Russia. They belong to three associations, according to Kielland-Lund (1981, 1994):

- *Eu-Piceetum* (EP). This is the most common forest association. EP is the typical climax community on nutrient poor to medium rich, podzolic soil types. EP is subdivided into sub-associations, e.g. *myrtilletosum* (= “spruce forest with bilberry”), *dryopteridetosum* (= “spruce forest with small ferns”) and *athyrietosum* (= “spruce forest with tall ferns”), with increasing soil richness and soil humidity (Dahl *et al.* 1986, Kielland-Lund 1994).
- *Melico-Piceetum* (MP). According to Kielland-Lund (1994), MP (= “spruce forest with low herbs”) occurs in warmer localities and on more calcareous soils than *Eu-Piceetum*, mainly in the boreonemoral and south boreal zones. MP has three main sub-associations: *pinetosum* (= “calcareous low-herb woodland”) on dry limestone soils, *typicum* (= “spruce forest with low herbs”) and *aconitetosum* (= “spruce forest with tall herbs”). Most *P. abies* forests have a trivial vascular plant flora, except *Melico-Piceetum pinetosum*, which houses, among others, rare and in some areas threatened orchids, e.g. *Ophrys insectifera* and *Cypripedium calceolus*.
- Kielland-Lund (1981, 1994) has described the association *Chamaemoro-Piceetum* on clay or thin organic soils. This community is called “spruce swamp forest”.

Norway spruce forest communities in the superhumid parts of central Norway differ from those described (Kielland-Lund 1981, 1994) in having frequent oceanic species: in the field layer, e.g. *Blechnum spicant* and *Cornus suecica*; and in the bottom layer, the sub-oceanic bryophytes *Plagiothecium undulatum* and *Rhytidiadelphus loreus*.

The most common types of central European spruce forest are the montane and the sub-alpine. Spruce also occurs in wide areas in lowlands with mixed woodland communities. It can be dominant at both the sub-montane and planar levels where there is low competition, e.g. around the edges of raised bogs, in acid marshy ground and on waterlogged soils. Four montane and sub-alpine *Vaccinio-Piceetalia* associations are described:

- *Piceetum montanum* (PM). According to Ellenberg (1988), PM occurs in the montane zone of the valleys of the Alps. PM has two main sub-associations: *galietosum* and *melicetosum* (= *Melico-Piceetum*). The slightly humid *galietosum* is found where the substrate is rich in bases. It has many herbs, predominantly *Galium rotundifolium*. The dry montane *melicetosum* is poorer in species. This type also occurs on bedrock, which is poor in bases, and even on dry slopes with relatively base-rich and loamy soils.
- *Veronico urticifoliae-Piceetum* (VP). VP is a special association of a more productive montane spruce wood type (Ellenberg 1988). It develops on acid soil where the water supply is somewhat better than that where *Piceetum montanum melicetosum* woods are found.
- *Piceetum subalpinum* (PS). In contrast to the montane spruce woods, the sub-alpine woods are as a rule poorer in species (Ellenberg 1988). These are more constant and may appear in large

numbers, e.g. *Oxalis acetosella*, *Vaccinium myrtillus*, *V. vitis-idaea*, *Calamagrostis villosa* and *Hylocomium splendens*. The spruce trees are mostly stunted because of severe winters. The type is common in central European highlands.

- *Sphagno-Piceetum* (SP) or *Piceetum subalpinum sphagnetosum*. This type, which has plants associated with wet conditions such as the genus *Sphagnum*, is found on waterlogged soils in all acidophilous spruce woods, especially in the sub-alpine region. It is frequent in high precipitation areas along the perimeter of the Alps.

The symbiotic relationship between the roots of Norway spruce and mycorrhiza fungi is important for spruce forest ecosystems. The importance specifically concerns Norway spruce in dry habitats, in habitats where soil moisture is variable, or generally in habitats with marginal growing conditions. In optimal growing conditions for Norway spruce, mycorrhizae are not so well developed. In dry habitats, mycorrhizae facilitate water uptake. Hundreds of species of mycorrhizae are described on Norway spruce.

B. Norway spruce as a key species

Norway spruce's importance for a very large number of species is due to its ability to change the soil, and to create essential structures owing to the size of individuals and their distribution in large continuous forests, as well as its dominance in creating dynamics in the landscape. In addition, Norway spruce as growing tree and decaying wood provides “home and food” for hundreds of species. In Fennoscandia and northern Russia, it dominates the forest landscape as the region's key species. In Norway, an estimated 20 000 species (~ half the number of species in the country) are associated with forests, a major part to spruce forests. Almost half the threatened species in Norway, Sweden and Finland (898, 695 and 717, respectively) live in forests (data from Nord 1994).

C. Special lichens

The spruce forest (called “boreal rain forest” or “coastal rain forest”) of the west central part of Norway is very rich in mosses, fungi and lichens. The latter group includes 40-50 species belonging to the so-called “Trøndelag element”. The lichen species either have their only known occurrence in Europe in this forest type, or have their main occurrence here (Holien 1996). A good indicator group for the occurrence of rare epiphytic lichens in the coastal rain forest is the *Lobarion* community, for which *Lobaria pulmonaria* is a characteristic species. In the alliance *Lobarion*, the epiphytes *Pseudocyphellaria crocata* and *Ramalina thrausta* are considered among the vulnerable Red List species of the coastal rain forest, whereas *Pannaria ahlneri* and “trønderlav” (*Erioderma pedicellatum*) are highly endangered. “Trønderlav” was classified as extinct in Europe until the summer of 1994, when it was found in two extremely small populations.

D. Special bryophytes

Norway spruce forests have a wide range of microclimatic and edaphic niches for bryophytes. Logs of Norway spruce at various stages of decay are habitats for many more or less specialised and very often rare communities and species of liverwort. Liverwort's occurrence on Norway spruce logs depends mainly on two factors: (i) the stage of decay (or length of time since the tree was felled) and (ii) the size of the log. Different species have different preferences. Larger logs have more species and larger populations. Typical Red List species living on decaying logs are *Lophozia ascendens* and *Calypogeia suecica*. The former is a vulnerable species with a preference for large young logs, while the latter prefers large old (heavily decayed) ones. Both occur mainly in the superhumid spruce forest of central Norway.

E. Interaction between planted Norway spruce forests and other forest types

The general consequences of artificial introduction of *P. abies* into deciduous forests are well known, especially from western Norway and central Europe (Ellenberg 1988, Fylkesmannen i Rogaland 1993). The high shade tolerance of *P. abies* gives it a competitive advantage over nearly all deciduous species, and over ground flora if the temperature regimes are favourable for Norway spruce. The microclimate becomes more humid and oceanic after introduction of *P. abies*. In addition, the humus becomes rawer and more acid. Changes in microclimatic and edaphic conditions result in sparse ground flora and fauna (Børset 1985). Under natural conditions there is a balanced dynamic in the competition between *P. abies* and trees and communities. However, when spruce stands are introduced outside their natural range of occurrence, the species can show unpredictable invasiveness.

F. Elements of boreal spruce forest ecosystems

Due to Norway spruce's dominant role in Fennoscandia and northern Russia, there should be a strong focus on the significance of the structure and dynamics of boreal spruce forests (Hansson 1992), especially in these areas.

G. Tree species

Different tree species are normally dominant at different succession stages. There are exceptions, however, in a few vegetation types in the boreal zone where the same tree species is both the pioneer and climax species. Spruce forests go through a deciduous stage (mainly birch, rowen, aspen, *Salix* sp. and alder in Fennoscandia) as the first step before the spruce becomes dominant. The biodiversity of the spruce forest depends on its succession stage (reviewed in Tømmerås 1994).

H. Deciduous trees in conifer forests

Deciduous trees lose their dominance in spruce forests after the pioneer period, but some of these trees are always part of the forest stand. The richer the vegetation type, the more deciduous trees are present. Old deciduous trees and large dead ones are very important for numerous lichens, insects and birds.

I. Period of rotation

Plant and animal species adapt to many niches, in a complicated pattern, during the forest's successive stages. Species that require very specific conditions may be dependant on the presence of burned trees, dead wood, small seedlings, or old but living trees. The effects of disturbances in the rotation cycle on species diversity are not well known (Hansson 1992).

J. Layers

From an ecological point of view, the existence of more than one vertical layer in forests is a key factor in determining an area's biodiversity. This layer structure is most dominant late in the pioneer and later stages.

K. Old trees

Spruce in natural forests may reach an age of 200-300 years. Usually some individuals become old and are of great size. These trees are habitats for many forms of life, such as woodpeckers, lichens, bryophytes and insects.

L. Dead trees

Dead wood results from various causes, including storm felling, fire, pathogens and normal ageing. This leads to a wide spectrum of types of dead wood being found in a spruce forest. Over a thousand plant and animal species take part in the process of decomposing dead spruce; a large proportion are specialists at a particular stage. It is estimated that more than 700 Norwegian beetle species are dependent on the dead wood of boreal forest tree species (Tømmerås, unpubl).

M. Continuity

Some areas in boreal forests are free from natural disturbances such as fire and storm felling. These forest areas can cover 20-40% of a forest landscape, and are often widespread on humid soil and in steep valley areas. Many cryptogams and invertebrates are dependent on continuous forest structure.

N. Importance of structural conditions and dynamic processes for plants and animals

The natural dynamics of spruce forests, in which a special mosaic landscape changes over time, leave some parts very little affected by disturbances (continuous forest) and other parts dominated by, for example, fires once every 100 years. Plant and animal communities adapt to these conditions. Many species are dependent on the stable structural conditions of a continuous forest, while others need disturbances such as fire (*e.g.* the threatened ortolan bunting *Emberiza hortulane* L., many insects and fungi) or storm felling. Finally, many species are dependent on the mosaic combination at the landscape level. Among these are the three species of forest hens: black grouse (*Tetrao tetrix* L.), willow grouse (*Lagopus lagopus* L.) and hazel grouse (*Bonasa bonasia* L.).

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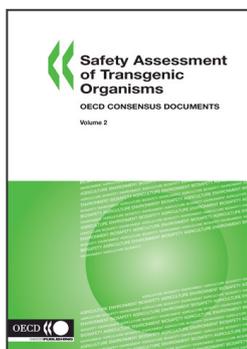
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