Ecology, history and silviculture of Scots pine (*Pinus sylvestris* L.) in western Norway – a literature review

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**Summary**

Results from a literature review on pinewood ecology, silviculture, genetics, aspects of history and forest resources of Scots pine (*Pinus sylvestris* L.) in western Norway are presented. The pinewoods cover ∼40 per cent of the forested land, ∼0.31 million ha. During the last 75 years, the area has increased by 17 per cent and the growing stock has risen from ∼10 to 34 million m$^3$. The impact of man in previous times was very marked, and has had a significant influence on the present forest conditions. The pronounced climatic gradients mixed with the topographic variation – from the coastal plains via the fjord systems to the high mountains – is reflected in rather steep gradients in the pine forest vegetation. Various floristic elements can be distinguished, from oceanic via the suboceanic in the outer islands to the thermophytic, boreonemoral and boreal elements in the inner fjord districts and valleys. The introduction of spruce (*Picea* spp.) plantations on 10–15 per cent of former native pine forests has not negatively affected the bird fauna at the landscape scale. Although not particular species rich, the pine forests harbour species usually not found in other forest types. So far, most work in the field of silviculture and forest ecology in the pinewoods of West Norway has been in the form of case studies. Implications of the results for forestry in the region are briefly discussed.

**Introduction**

In a Eurasian perspective, western pinewoods are unique, representing spectacular environments, rare wildlife and vegetation and cultural heritage while also supplying the wood industry with valuable raw materials. Today, spontaneous oceanic Scots pine forests are only distributed in Scotland and western Norway. The research on Scots pine forests in West Norway has varied from time to time (Robak, 1960). Especially during the first 10 years of the Forest Research Station in West Norway, 1916–1926, studies of flowering, seed production, cultivation methods, provenances,
forest production, forest damages and stand treatment in the pine woodlands were initiated. The attacks of the pine needle cast fungus (*Lophodermium pinastri*), which during the years 1921–1923 nearly devastated the coast plantations of non-coastal pine, clearly reduced the popularity of Scots pine in tree planting during the 1930s and 1940s (Magnesen, 1992). The research activity on the pinewoods in West Norway from the 1950s up to the 1990s must be regarded as modest, mostly due to the fact that the afforestation process, and hence the forestry research, concentrated on planted Norway spruce and exotic conifers. In the 1990s a new focus of developing a more sustainable forestry emerged, and projects dealing with the importance of spontaneous pine forests and effects of the spruce plantations upon biodiversity were initiated. A great deal of the previous results on Scots pine have only been published in Norwegian reports, thesis, textbooks and magazines (in Norwegian), of which some might be of interest to a broader audience. The main purpose of this review is to present literature of Scots pine in silviculture and forest ecology, mainly based on the forestry research and experiences in West Norway.

### Geographical and altitudinal distribution, resource situation

Western Norway includes a total land area of 5.85 million ha over four counties, of which 0.94 million ha is productive forest land. The region stretches from 58° 20′ to 63° 30′ N, and from 5° to 9° E. The region harbours five major fjord systems (Figure 1).

Scots pine is presently distributed in most parts of the region, even though the pinewoods are rather scattered along the coastline and on the islands (Robak, 1960). Larger woodlands of a thousand hectares or more only occur in the more protected fjord and valley districts. About 99 per cent of the pinewood area is naturally regenerated semi-natural forest, whereas the plantations cover ~3000 ha – mostly located in the coastal districts (Øyen, 1998). Scots pine is found throughout West Norway from sea level to 1100 m elevation, on the highest mountain plains only as saplings. In the southern, coastal mountains the upper timberline of Scots pine is ~400 m, and it decreases to ~300 m in the northernmost districts. The timberline rises to ~550 m in the middle fjord districts, and reaches its maximum of 900 m in the inner fjords of Sogn (Ve, 1930, 1940; Ekrheim, 1935; Tollan, 1937; Robak, 1960; Holten, 1986). In the most recent geographical floristic classification, the pinewoods are represented in boreonemoral, south-boreal, middle-boreal and north-boreal vegetation zones (Moen, 1998). Pinewoods along the coast and fjord districts located west of the climatic boundary ‘annual precipitation above 1200 mm, average air temperature above 0°C in February’ are classified as oceanic pine forests. Conversely, pinewoods in the inner fjord districts and valleys are referred to as boreal pine forest types (Øyen, 1998).

Forest inventories during the last 75 years show that the pinewoods in West Norway have increased substantially. The first forest inventory in the region was made in the late 1920s, as a part of the national forest inventory (Skøien and Vigerust, 1933). The pinewood area covered ~0.25 million ha and the growing stock accounted for 10 million m$^3$ (excluding bark). The latest inventory in the mid 1990s shows that forest area has increased to 0.33 million ha and growing stock is now 34 million m$^3$ (Tomter, 2000). In the late 1990s the annual harvested volume was less than 0.2 million m$^3$ and the annual increment ~0.7 million m$^3$. Due to the low utilization, we can expect a further accumulation of timber in the years to come.

### Aspects of Scots pine history

According to pollen records Scots pine colonized West Norway ~9000 BP (Fægri, 1935, 1940, 1943, 1950), following the spread to East Norway from Sweden and Denmark (Gjære, 1992). The first large-scale deforestation in West Norway took place ~2500 BP when the climate turned cooler and moister (Fægri, 1940, 1943). The man-made conversion of coastal forests into heathland lasted for many hundred years – in some sites coastal forest was even cleared and burned in the late nineteenth century (Kaland, 1986). However, in most landscapes a certain tree cover has been retained, despite heavy cutting,
grazing and burning. Wood, as a central trade product from West Norway, dates at least back to the twelfth century (Tveite, 1961; Fryjordet, 1992; Frivold, 1999).

Several activities relied on significant resources of wood, such as iron production, salt production and during the seventeenth century also the copper mining industry. The first water-driven sawmills in West Norway were established in the mid-sixteenth century. The utilization of woodlands continued after the first settlements, but strongly increased after the export of balks, boards, planks, tar and boats to Scotland, England, The Netherlands and other European countries expanded during the seventeenth century (Smout et al., 2004). Within a 50-year boom-period from 1600 to 1650, there was a huge increase in sawmills in the southern parts of the region (Tveite, 1961). About 100 years later the bulk of the activity moved towards central and southeast Norway, leaving only the sawmills located in the inner fjords active (Grüner, 1972; Fryjordet, 1992).
During the first half of the eighteenth century most of the export from West Norway was suspended owing to strict forest regulations, but most likely due to the lack of mature pine timber resources (Monrad-Krohn, 1976). The human population increased rapidly—the wood and timber resources, mostly Scots pine, became gradually in shortage. During the period 1750–1900, most of the cutting took place in rather remote areas, far away from the sawmills and ports. The small-scale farm industry based on pinewood resources was to a greater extent directed towards the regional market. In the second half of the nineteenth century, tree planting became more popular, and the first initiatives for plantation silviculture were made (Gjerde et al., 1996; Øyen, 1998).

Genetics and colonization of Scots pine in West Norway

Most palaeobotanical studies in the region indicate a spread of Scots pine from east to west over the mountain passes running north-south (i.e. Moe, 1979; Jakobsen and Follum, 1998). However, an additional colonization route into the Scandinavian Peninsula from northeast via Finland has been suggested based on variation in seed-transmitted mitochondrial DNA (mtDNA) (Sinclair et al., 1999). Variation in mtDNA in northern Europe is not consistent across experiments (Sinclair et al., 1999 vs Soranzo et al., 2000), however, and a dual migration of Scots pine into Fennoscandia has not been generally accepted. The need for analysing more populations for tracing the post-glacial history of Scots pine in Scandinavia is clearly evident (cf. Soranzo et al., 2000).

In 1916 a provenance trial was established in West Norway for finding appropriate provenances for a northern coastal climate (Hagem, 1924). Provenance origin was found to be very critical for survival, and the coastal provenances included were superior in this respect. The more eastern and continental the origin—the more injury, and survival declined substantially with an east-west transfer of only 80 km (Hagem, 1924, 1926). Conversely, coastal provenances performed poorly and continental better in another trial established in the continental part of eastern Norway (Dietrichson, 1968). An underlying cause of mortality and injury in these experiments was inadequate synchronization of the growth rhythm with the climate. Plants injured by frost or desiccation during active growth were much more susceptible to subsequent fungus attack, such as by Gremeniella abietina and Lophodermium seditiosum (Dietrichson, 1968; Magnesen, 1992). The general finding reported here from Norwegian experiments, of strong local adaptation and sensitivity to transfer of provenances (Hagem, 1924; Heiberg, 1938; Dietrichson, 1968; Magnesen, 2001), is typical for Scots pine trials with extreme site conditions (high altitudes, maritime or boreal), such as those in Scandinavia (Giertych, 1991). On a European scale, however, Scots pine is distinct from other trees by the general better performance of local vs non-native populations (Giertych, 1991).

The strong differentiation in adaptive traits is surprising considering the effective pollen flow in Scots pine (Lindgren et al., 1995), and the concordant lack of allozyme differentiation, as reported in Sweden (Gullberg et al., 1985). In West Norway, however, mountains and fjords may act as barriers to gene flow and favour small-scale differentiation (cf. Eriksson and Ekberg, 2001). Similarly, different timings for the maturation of male and female flowers across the climatic gradients of a variable landscape (Strand, 1957) may create partial genetic isolation and differentiation (Gullberg et al., 1982; Savolainen, 1996; Ohlson, 1999). Dual migration from different glacial refugia, as indicated above (Sinclair et al., 1999), could imply a genetic divergence between Scots pine on either side of the north-south directed mountain chain of southern Norway.

As Scots pine was an early colonizer, these evolutionary forces and topographic circumstances have been allowed to work for ~9000 years, and have possibly contributed to the present strong genetic differentiation of the species. Differentiation at a similar spatial scale has also been reported in Douglas-fir in north-west America (Pseudotsuga menziesii), where movement of seedlings from north- to south-facing slopes at the same elevation lead to ~80 per cent of the seedlings being poorly adapted (Campbell, 1979). The most recent recommendations in Scots pine in West Norway are to use seed sources only
within strictly defined seed collection regions, and to avoid movement in elevations beyond 200 m (Magnesen, 2001).

**Pinewood vegetation and soil**

Fremstad (1997) has presented a comprehensive work on physiognomic and vegetation types in Norway. The classification of pinewood vegetation in West Norway is based on reviews and studies from Kielland-Lund (1967), Aune (1977), Bjørndalen (1980), Omberg (1981), Sekse (1981), Bakkevik (1984), Øvstedal (1985) and Moe et al. (1992). The following main types are identified on productive forested land (i.e. Larsson et al., 1994; Fremstad, 1997):

- Lichen woodland
- Cowberry–bilberry woodland
- Heather–bog bilberry woodland
- Bilberry woodland
- Small-fern woodland
- Low-herb woodland
- Calcareous low-herb woodland
- Tall-herb woodland

Owing to the human impact and the biogeographical gradients, the classification into subassociations or vegetation types can be rather difficult (Øyen, 1998). In most sites, it seems clear that competition and co-dominance of downy birch (*Betula pubescens* Ehrh.) and juniper (*Juniperus communis* L.) are the normal features. Especially during early successional phases, a minor occurrence of rowan (*Sorbus aucuparia* L.), alder (*Alnus* sp.), aspen (*Populus tremula* L.) and goat willow (*Salix caprea* L.) is common. On fertile sites, a mixture of pine, oak (*Quercus* sp.) and hazel (*Corylus avellana* L.) is frequent, mainly in coastal sites and south-facing lowland slopes. In the inner fjords and valleys, mosaics of Norway spruce (*Picea abies* L. Karst.) and Scots pine may develop in the climax phase, mostly on poor sites (Nedkvitne and Thomter, 1953). However, this mixture is rare; spontaneous Norway spruce only occupies 3000 ha in West Norway.

Xerophytic, herb-rich pine forest types are sporadically found on calcareous rocks: Saniculo–Pinetum (Bjørndalen, 1980), and typically rare species associated with rich deciduous woodlands. Herb-rich and mixed stands of Scots pine on fertile ground with one or more of the following species, *Alnus* sp., *Betula* sp., *Fraxinus excelsior* L. and *P. tremula* L., are often classified low-herb woodland.

In the oligotrophic pinewoods of West Norway, acidic and impoverished soils with podzol profiles are the most common, especially in cowberry, heather–bilberry and bilberry vegetation types. Surface pH is consistently low, and there is marked leaching with a prominent E layer and deposition horizons with humus and iron. In a survey of 20 mature pine stands in bilberry and small-fern vegetation types, average pH in the humus layer was 4.0, loss of ignition 70 per cent and the Kjeldahl nitrogen content was 1.2 per cent. Average pH in the B horizon was 4.8 and the content of nitrogen 0.2 per cent (Nordvik, 2000). Scots pine seems to be most stable on sharply draining soils, although it is found on a great variety of bedrocks and soils (Nilsen, 1936).

**Seed production and mast years**

The pioneer work of Hagem (1916) demonstrated that Scots pine needs a minimum summer air temperature (June to August) of 10.5°C to produce viable seeds. Owing to cone collections and observations in West Norway from the late nineteenth century to 1916, he also claimed that Scots pine in the lowlands produce some viable seeds every year – with the highest seed production in the inner fjord districts. Mast years occur with an interval of 3–4 years – somewhat less frequent in high-altitude sites. These results were later supported by seed collections in two mature stands in inner fjord districts, Voss and Sogndal, between 1959 and 1970. Seed rain up to 500 seeds m⁻² year⁻¹ was reported, with an average of 164–184 seeds m⁻² year⁻¹ (Koski and Tallqvist, 1978). However, lack of seed rain might be an obstacle in other sites. In the work of Øyen (1997b), in oceanic pine stands, several years and stands occurred with no viable seeds. These results highlight the need for timing of the coning, cutting and scarification – to secure proper effects of soil tillage and seedbed preparation in the regeneration process.
Scots pine regeneration – disturbances

Scots pine in West Norway forms both even-sized and more irregular stands. In sites subjected to disturbance regimes like severe wind damages, crown-fires and avalanches, even-sized or two-storied stands are most common. Forest fires, covering areas up to some hundred hectares, are quite frequent in the southern, densely populated part of the region, more rare further north (Skre et al., 1998; Øyen, 1999). In areas subjected to smaller events (death caused by less severe wind damages, snow breaks, insects and fungi), or in stands that are regularly cut above a certain target diameter, more irregular age structures seem to occur. Age structures in smaller forest stands could display a wide variety of distributions (Øyen, 1997b). Age class peaks ∼100–150 years seem common in mature pine stands. Mixtures of pioneers, more than 200 years, embedded in a matrix of offspring ∼100 years old are also indicated (Moe et al., 1992). A recent work over 1.5 km² in Kvam, Hordaland, showed a rather irregular age structure, where trees up to 500 years occur (Gjerde and Baumann, 2002). Also, in mountain pine forests the age structures show missing age classes – an indication of heavy cutting and/or climatic unfavourable conditions. Tree ring chronologies from Scots pine are commonly used for historical climatic information (Brandt, 1975; Kalela-Brundin, 1999). Pine trees up to 700 years are reported (Skar, 1964).

Øyen (1997b) demonstrated that climate, soil, humus and vegetation in West Norway are far from optimal for regeneration of pine, except in the few most favourable sites in the inner fjords and valleys. Even in the best pinewood areas of the inner fjords abundant regeneration occurs only in the south-facing slopes where litter breakdown is extremely rapid and where the seeds are allowed to germinate in almost pure mineral soil. On considerable areas, scarification or burning combined with sowing or planting is necessary for successful regeneration, and to meet the quality and production goals set for a sustainable forestry. Especially on fertile soils, there is a great risk for failures in natural regeneration due to weed competition and frost heaving (Øyen, 1997b). Locally, native pine is reported to suffer from red-deer browsing (Veiberg, 1999), which severely can hinder regeneration where conditions are otherwise suitable.

Yield and forest production, silvicultural methods

The first long-term growth and yield plots were established in 1915 (Smitt, 1926). The first yield tables, based on an extended collection from pinewoods in the region, were published in the 1960s (Bauger, 1965). Most stands display a yield of 3–6 m³ ha⁻¹ year⁻¹, with the highest yield class (YC 10) in fertile soils in warm south-facing lowland slopes in the continental districts of Sogn and Nordfjord, Sogn og Fjordane. Observations in about 100 long-term plots in Scots pine stands in West Norway show a maximal basal area of 69 m² ha⁻¹, and a maximum standing volume of 730 m³ ha⁻¹ (Skogforsk, 2005). Øyen (1997a) found that the bulk of stands in West Norway had a height and volume development that fitted well the growth models from southeast and central Norway. However, windswept sites in coastal areas had a more moderate height-age development, and also a slightly lower volume increment. A comparison of neighbour stands of Scots pine, Norway spruce and other tree species in West Norway showed that spruce on average was twice as productive as pine. Downy birch had a stem volume production of 73 per cent compared with Scots pine (Øyen and Tveite, 1998).

In general, clear-cuts or the seed tree method is mostly applied in the final felling. In windswept sites, small clear-cuts (0.2–1.0 ha) are the most common and also the most recommended method (i.e. Hødal and Smitt, 1921; Øyen, 1997b). In protected fjord pinewoods, 40–50 seed bearers ha⁻¹ are left behind – often combined with scarification (Øyen, 1997b; Bergheim, 2002). Selection cutting, group system and two-storied uniform system are rarely applied, although suggested to be more common in future silviculture (Levende Skog, 1998).

Biodiversity patterns in the pinewoods of West Norway

The coastal part of West Norway, characterized by a pronounced oceanic climate, has a distinct
Atlantic biogeographic element where lichens and bryophytes are the most important groups, particularly with regard to the number of red-listed species (Blom et al., 2002). There is, however, probably no endemic species in this region, and the oceanic flora element is best regarded as an impoverished subset of the oceanic flora of the British Isles. The classic work of the oceanic lichen element in Scandinavia is that of Degelius (1935), but he only included macrolichens. Jørgensen (1996) included all lichens and added several newly discovered species to this element. The autecology and geography of the oceanic mosses in Norway were treated by Størmer (1969), whereas detailed information on the ecology and distribution of the oceanic hepatics can be deduced from the floristic work of Jørgensen (1934).

In a recent project, biodiversity patterns in six study areas in different parts of Norway were mapped. In all areas detailed surveys of vascular plants, bryophytes, lichens and polyple fungus were carried out. One of the study areas consisted mainly of oceanic pine forest and was situated in Kvam, Hordaland County (Gjerde and Baumann, 2002; Gjerde et al., 2004). In this area also the forest floor fauna of snails, spiders, carabid and staphylid beetles, as well as the canopy arthropod fauna of pine trees, were investigated. Data from the study made it possible to compare the biodiversity of oceanic pine forests with other forest types as well as pine forests in other parts of Norway.

In general, pine forests had lower species richness than spruce forests and deciduous forests. This is partly because pine forests normally are found on low-productive soils, and forests on these soils harbour a lower number of species than those on high-productive soils (Gjerde et al., 2005b). However, not all taxonomic groups fitted this pattern. In Kvam, species richness of spiders was higher in low-productive pine forests than in high-productive temperate deciduous forests (Sætersdal et al., 2003). Because natural spruce colonization has not reached the area, pine forests are found on more productive soils that are usually occupied by spruce forest in other parts of Norway. Among the taxonomic groups studied in Kvam, vascular plants and bryophyte species was also higher in Kvam (Gjerde et al., 2004). These patterns, however, resulted mainly from abundant calcareous microhabitats present also in low-productive pine forests in Kvam.

In summary, oceanic pine forests of western Norway are expected to be more species rich than pine forests in eastern Norway primarily because oceanic pine forest on average is found on more productive soils (Gjerde et al., 1996). Furthermore, some groups of species (e.g. oribatid mites) are favoured by the humid climate and mild winters of the oceanic pine forest. Although pine forests cannot compete with the more productive forest types regarding species richness, it is important to notice that pine forests represent the most important habitat for several species. Some of these species mainly, or only, found in pine forests are red-listed species. In a study of lichens on hazel (C. avellana L.) stems in Kvam, Hordaland County, Ihlen et al. (2001) found that although the total number of lichens was higher on hazel in temperate deciduous forest compared with pinewoods, the number of microlichens was higher on hazel located in pine forests.

In a recent study of the arthropod fauna of a total of 24 Pinus sylvestris trees, 18 trees in southeast Norway and 6 trees in West Norway (Kvam, Hordaland County) were examined, the latter in the oceanic pine forest. Trees identified to two age classes, mature (60–120 years) and old (250–330 years), were treated with a synthetic pyrethroid. The knocked-down arthropods were collected in plastic funnels that were placed on the ground. More than 30,000 specimens were found, covering 96 per cent of the collected arthropod biomass (Thunes et al., 2004). Altogether, 512 species of arthropods were identified. Of these, nine species were new to science (five Diptera and four oribatid mites); 2 species were new to the European fauna, 3 to the Scandinavian fauna and 82 species were reported in Norway for the first time. Faunal differences were rather large between the two sites as only 93 species were common to both localities. The study indicates that there exists a proportion of the fauna associated with old trees, but that these species are generally rare in the landscape. Hence, these differences can be explained by the scarcity of old trees, habitat heterogeneity and structural differences between old and mature trees (Thunes et al., 2003).
Avian diversity patterns in the native pine forests

Two studies have addressed the question of potential effects on the diversity of birds of spruce plantations in the oceanic pine forests of West Norway. The first study (Gjerde and Sætersdal, 1997) compared diversity of birds in 35 plots of 58 ha each. Within each plot 18 circular subplots of 50-m radius were used to count passerines. The plots were stratified from pure native pine forests, through different mosaics of native pine forests and spruce plantations, to pure spruce plantations. Bird species richness was higher in pine forest than in spruce forest. However, the highest species richness was found in a mosaic forest of native pine and spruce plantations. It is argued that when mixing pine forest and spruce plantations, species richness is increased as a result of mixing of species confined to each of the two forest types, as well as the species favoured by the mixture of pine and spruce forest.

At present –13 per cent of the productive pine forest of West Norway has been converted to spruce plantations. As a result, the bird species richness has been reduced locally (at the stand scale). However, at the landscape and regional scales the richness has increased. Typical examples of bird species increasing in western Norway as a result of introduced spruce plantations are coal tit (Parus ater L.) and nutcracker (Nucifraga caryocatactes L.).

The second study aimed at investigating the effects of spruce plantations on two internationally threatened or vulnerable species. These species are the white-backed woodpecker (Dendrocopos leucotos Bechstein) and the grey-headed woodpecker (Picus canus Gmelin) (Gjerde et al., 2005a). Although overall species richness is not reduced by spruce plantations, it is possible that these two threatened species may be negatively affected. The densities of the two species were investigated in 100 forest landscapes (100 ha each) with different proportions of native pine forest and spruce plantations in western Norway. No clear threshold values were found with respect to the proportion of spruce plantations. However, both species were extremely rare in plots with more than 60 per cent spruce plantations.

It is concluded that the proportion of spruce plantations should be stabilized at moderate levels to secure viable populations of the two threatened woodpecker species. Presently, owing to the more favourable economy in harvesting dense spruce plantations compared with the rather open grown native pine, there are no indications that the proportion of spruce, on a regional level, will exceed 15 per cent of the productive pine forest.

Conclusions

1 Most previous studies in the pinewoods of West Norway must be regarded as case studies – especially when we take into account the extreme gradients in climate, soil condition and topography.
2 Scots pine seems to be well adapted to infertile soils, although occupying and thriving also at more fertile sites in West Norway. The best conditions for growth and regeneration are mainly found in the inner fjord districts.
3 Studies including age structures indicate that pinewoods in West Norway could be subjected to major site disturbances as well as minor disturbances. By applying a wide range of silvicultural methods, the complex structural patterns might be mimicked.
4 Although man has greatly affected these forests by cutting, grazing and burning, especially in previous times, the pine forests still have many natural characteristics, and the pinewood area and the growing stock are increasing substantially.
5 In general, the pinewoods display fewer species of vascular plants, lichens, mosses and polypore fungi than deciduous forests. Still, western pinewoods have a rich flora of bryophytes and lichens, and contain important habitats for several red-listed species. A recent study of the arthropod fauna associated with pinewoods indicates a high diversity.
6 The present conversion of native pine to spruce plantations (10–15 per cent) does not negatively affect a diverse bird fauna at the landscape scale.
7 Needs in future research are many – i.e. to further develop a sustainable forestry, to apply appropriate silvicultural methods and to identify and preserve genetic diversification and biodiversity in the western pinewoods.
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