

Changes in Wood and Stem Properties of *Pinus sylvestris* Caused by Provenance Transfer

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Wood properties focused in forest tree breeding should be of economic importance, have a large total variation and a high heritability. The properties of interest are those that influence the strength and durability of sawn products or the amount and properties of pulp produced. The following wood properties are treated: width of the annual ring, juvenile wood, late wood content, heart wood, tracheid dimensions, basic density, stem straightness and branch diameter.

The provenance variation in wood properties can be related to differences in growth phenology. In the northern part of distribution *P. sylvestris* (*L.*) provenances transferred a few degrees southwards have a high survival and yield but stem wood production is low. Trees from these provenances will be straight and with few spike knots or other injuries. The shoot elongation period will be short and the temperature sum required for wood formation sufficient. Provenances transferred southwards will form thin annual rings, few and thin branches, little early wood, high basic density and slender tracheids with thick cell walls in comparison to local provenances. An example of the effect of alternative transfers on the yield and wood properties is evaluated. In regions with deviating climatic patterns alternative provenance transfer patterns may be better. The objectives of the land owner should influence the provenance choice. The importance of integrating tree improvement with silvicultural management is discussed with reference to spacing.

Keywords *Pinus sylvestris*, provenance, yield, silviculture, wood properties, growth phenology

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1 Introduction

Before starting the crusade to improve wood and stem properties the “eager beaver” pine breeder should stop and ask himself a few important questions. Among these questions are which properties should be improved, what levels of improvement that are necessary to achieve and whether or not there will be a stable demand for the goods delivered in the future. Another question of principal interest is if the breeding objectives should be directly aimed at improving wood properties or at facilitating silviculture with similar objectives. Although the final outcome may be the same the methods and objectives used may be quite different. Finally and perhaps most important of all is the question of what level of selection or what breeding method should be used to achieve the objectives. This paper has the focus concentrated to the provenance level.

Pinus sylvestris (L) is distributed over much of boreal and temperate Eurasia (Boratynski 1991). In the northern part of its distribution we find a low degree of population differentiation, the majority of genetic variation found within populations as well when using isozyme studies (Gullberg et al. 1985, Prus-Glowacki 1991) as when assessing survival and wood production (Eriksson et al. 1976, 1987). The continuous distribution of the species and the absence of effective pollen barriers make possible the intense pollen flow over great distances that could explain this (Koski 1970). Clinal variation has been demonstrated for most properties in this region (Langlet 1959). In central Europe the variation has been regarded as ecotypic (Giertych 1991) probably due to larger variation in altitude and climate and a less continuous distribution. Though most of the clinal variation has been latitudinal, also altitudinal, longitudinal and coastal–continental variation have been reported (Giertych 1991).

2 Market Trends

Looking at the wood utilities market for Scots pine there are some trends that seem to be more or less permanent. There is an increased demand

for homogeneity from the manufacturer. At present the pulp industry can utilize almost any wood based raw material as long as it is sufficiently homogenous. The same demand applies for sawn products. As an example the grading of structural lumber must be made so that the weakest board meets the standard required. Thus, the majority of boards will actually be much stronger than required. The problem is that wood by nature is anything but homogenous. Wood properties vary within trees, between trees, between stands and regions (Zobel and van Buijtenen 1989). Increased uniformity and thus greater utility is by itself an objective. Another trend that can be related to homogeneity of wood is the prize increase from damaged and injured wood through sound wood with knots to straight grained wood free from knots. A third trend relates to the reduced storage of wood at the industries. Reduced storage is an economic necessity and in many industrial processes only fresh wood can be used. Nowadays the only place where timber storage is accepted is as standing trees. These changes all work in favour of the tree breeder. Through breeding he can help increasing homogeneity within stands and improving wood properties. He can also predict the future wood properties of standing pines.

Looking at forestry the fourth trend is “back to nature”. Natural regeneration, ecosystem management and the use of alternative methods to the conventional clear felling and planting forestry, all this reduces the conventional pile of work and financing for Scots pine breeding. The majority of forest tree breeders must find use for their competence by adapting to the new opportunities instead of going on as if nothing had happened.

3 Wood and Stem Properties

Wood and stem properties utilized in forest tree breeding should be of economic importance, have a large total variation and a high heritability. The properties of interest are those that influence the strength and durability of sawn products or the amount and properties of pulp produces. The uncertainty about future changes in industry con-

sumption and the extended time perspective makes specification difficult. For instance differences in aesthetic consumer preferences are difficult to include in a breeding programme. The following properties should be of interest for most industrial uses of Scots pine in future. The list is based on interviews with manufacturers of sawn goods and pulp. In their review of inheritance of wood properties in Scots pine Ståhl and Ericsson (1991) have made a more detailed description.

Undamaged wood. Trees that have been affected by pathogens, wind, frost, drought, mechanically or otherwise will frequently be damaged. The damage could be caused by the affecting agent, alternatively by a responsive action of the tree. Decays, shakes, ingrown bark, pitch pockets and reaction wood are decreasing the homogeneity of wood and are also disadvantages for most industrial users.

Wood density. Although basic density or specific gravity is a complex property it is primarily determined by three wood characteristics, late wood content, cell size and cell wall thickness (Zobel and Talbert 1984). In spite of this basic density is treated as a single property in most breeding programs. Wood density is directly related to the amount of chemical pulp produced. Below certain minimum levels the timber processing is rendered difficult and the strength of sawn goods is reduced.

Stem straightness and reaction wood. Crooked lumber will reduce yield and make debarking and processing difficult. It is important to remember that any deviation from straightness corresponds to a change in wood properties. If reaction wood (i.e. compression wood) has occurred pulp properties will change and sawn goods may twist. Tracheids are short while lignin content and fibril angle are high and the cellulose content low. As sawn goods are dried longitudinal shrinkage occurs.

Juvenile wood. The juvenile wood, formed closest to the pith, has properties deviating from mature wood formed by an older cambium (Rendle 1960). The combination of the two in the same piece of wood make it more difficult to process. Juvenile wood is undesirable for use in most solid wood products as well as in pulp (Haygren and Bowyer 1982).

Early wood content. Early wood is formed in the beginning of the growing season when there are high auxin levels but the amount of photosynthesis available for cell wall formation is limited (Zimmerman and Brown 1971, Menyailo 1985). In comparison to late wood, early wood has shorter wider tracheids with thinner cell walls. The pulp yield is smaller and sawn goods have reduced strength when early wood content is high.

Tracheid properties. Stem tissue consists primarily of tracheids. The size and properties of tracheids are therefore major determinants of wood quality. For most pulping purposes a long slender tracheid with thick cell walls is the optimum although shorter fibres could substitute pine tracheids in some products.

Heart wood. The formation of heart wood starts once the active processes in the wood have stopped. The amount of heart wood formed at a given age is dependent on the growth rate of the tree. The heart wood, formed close to the pith in older trees, has special properties and a deviating chemical content. Durability and stability of sawn goods with heart wood included is increased.

Knot diameter, angle and quality. For all practical use few knots are preferred to many, thin knots to thick knots and sound knots to dry knots or decayed knots. The knot angle is of importance as the crosscut of a straight angle knot will cover a smaller area of sawn goods than that of an acute angle knot.

Stem form and taper. Looking at stem form, large dimensions and minor taper reduces cost of procurement and makes alternative end uses possible. The most versatile properties are found in annual rings formed at mature age. A large part of this wood is used for fuel and pulp if logs with major taper are sawn using present methods.

Annual ring width. Annual ring width simply reflects the annual diameter growth. The only direct effect on the properties of wood is the cosmetic effects on sawn timber and veneer.

In spite of this, the annual ring width is included in most calculations of assortments used today since it is correlated with other properties directly affecting wood properties. Positive correlation has been found between width of the annual ring and branch diameter (Persson 1976), knot content, lignin content and pentosane content

and negative correlations with basic density, percentage of heartwood, percentage of latewood, extractives content, pulp yield and the bursting and tearing strength of pulp (Ericson et al. 1973). In general, pines with wide annual rings tend to have low basic density, thick branches, low percentage of late wood and heart wood, short and thick tracheids and a high percentage of juvenile wood, the net result being poor quality sawn timber and low pulp yield per unit of wood (Ståhl and Ericson 1991).

It is tempting to conclude that a tree breeder aiming at increased production of Scots pine would create a similar reduction in wood quality. There are however at least three reasons that this must not be the case.

- The relationships between growth rate and wood properties are not strong. As argued by Zobel and Talbert (1984) through a careful combination of selection criteria high growth rate and good wood properties can be combined.
- The effect of annual ring width on wood properties varies during a full rotation. In Fig. 1 is indicated the variation in annual ring width during a full rotation. An increase in diameter growth rate during the first third of the rotation will deteriorate wood properties as argued above while the same change at the end of a full rotation could improve wood properties. Increased growth rate at the end of rotation will increase the amount of knot free wood found in annual rings formed at mature age. To produce as wide annual rings at the end of rotation as during the first third of the rotation is virtually impossible in practice (Persson 1992, Eriksson 1993).
- A third and important fact is that while there is a negative relationship between annual ring width and desirable wood properties this is not necessary so for height increment or total volume production per hectare. As examples height is positively correlated to stem straightness (Prescher and Ståhl 1986) and tracheid length (Ståhl 1988). In the severe climatic conditions of high altitudes in northern Sweden Ståhl et al. (1986) argued that a breeding programme aimed at increased survival and wood production would also lead to improvements in wood properties.

Therefore one can not simplify the problem by concluding that a fast growing tree or stand has

worse wood properties than a slow growing tree or stand, although this may often be the case. In fact, one of the essentials of forest tree breeding is to identify and put to use the trees that combine fast growth and favourable wood properties. The strive to find crop ideotypes (Dickmann 1985), genotypes that are high-yielding when grown in stands, leads to improvement of wood properties. Genotypes with high harvest index (Donald 1982) have proportionately few and thin branches, which is positive both to areal stemwood productivity and wood quality. An example is plus tree E 1101, the “Kanerva”-pine, utilized in the Finnish tree breeding programme (Kärki 1985, Pöykkö 1993).

As summarized by Ståhl and Ericson (1991) the wood properties mentioned above are all of economic importance having a large total variation and a relatively high heritability. In spite of that, in a breeding program the number of properties selected for should be kept at a minimum. If not, the improvement in each trait may be too limited. In Table 1 an attempt is made to limit the number of properties.

In most breeding programmes a concentration to survival, basic density and branch properties would be sufficient. There is a significant correlation between survival and frequency of undamaged trees (Persson and Ståhl 1993). Improvement of wood properties could be made by using material with sufficient hardness to keep stand density high and frequency of damaged trees low while using silvicultural means to reduce early growth potential and utilizing late growth potential. The obvious risk with this strategy is that early stand density will be reduced and the blame for decreased wood quality put on the forest tree breeder. Increased survival should not be used to decrease stocking levels if good wood properties is a main objective. With these limitations in mind the forest tree breeder working in cooperation with silviculturists may be satisfied. Additional gains could be achieved by selection for increased density and improved branch properties. The results from the Swedish tree improvement programme indicates that wood production and branch properties could be simultaneously improved. In the Swedish program the productivity increased while branch diameter decreased but the number of branches/whorl

Table 1. Relationship between survival, early and late growth potential and different wood properties possible for selection.

| Survival | Early growth potential | Late growth potential |
|----------------------|--|--|
| Injuries and damage | Annual ring width Branch properties | Stem form and dimensions Juvenile wood content |
| Spike knot frequency | Early wood content | Amount of knot free wood Basic density Tracheid dimensions |
| Stem straightness | Cell wall thickness | |

was increased (Andersson 1986, Wilhelmsson and Palmér 1988).

Provided that assessment of wood properties could yield new and better information than today there could be alternative approaches with a great potential for wood improvement. Methods are developed. Among these are X ray computed tomography (Lindgren 1991, Lindgren et al. 1992), microdensitometry (Polge 1963) and fiber structure analysis of wood cross-sections using high resolution microscope and image analysis. As an example, the last method is developed at our department. By assessment on increment cores annual ring width, early wood content, cell wall thickness and variation in tracheid dimensions will be estimated.

4 Interaction of Site, Silvicultural and Genetic Effect

In a general comparison of site-, silviculture- and seed source- effects site would have the strongest effect on wood properties in the majority of cases comparing the effect of provenance variation to site variation. Ståhl et al. (1990) examined the frequency of spike knots in different provenance trials. Although under genetic influence the majority of variation could be attributed to site conditions. In their study of the effect of climate and provenance transfer on stem quality of Scots pine in northern Sweden, Persson and Ståhl (1993) found the number of un-

damaged stems to be gradually decreasing towards a more severe climate, but the residual site to site variation was large. In a study of *P. contorta* (appendix by Eriksson in Ståhl and Persson 1988), tree volume functions were developed, differentiated by site and provenance. There was no significant variation in stem form (i.e. form of function when height and DBH are the same) between provenances but significant site variation.

5 Provenance Variation in Wood Properties

Provenance variation in wood and stem properties can be related to differences in growth phenology. To maximize the survival and growth while minimizing injuries and keeping wood properties good a well adapted provenance growth rhythm is essential. The longer the growth period the higher the growth potential, but a long period of active growth increases the risk of damage in spring, autumn and during cold winters. As late wood formation is an active process succeeding shoot elongation a long period of active growth or a short growing season may leave little time for late wood formation (Ericson et al. 1973). Several studies have shown that growth cessation and winter hardening are controlled by photoperiod and temperature (Langlet 1936, Dormling 1971, Sarvas 1974, Koski 1985).

In the northern part of distribution Scots pine

Table 2. The calculated effect of latitudinal provenance transfer on different traits at age 28 years. Applied stored location is 64° N 200 m.a.s.l. Traits included are height, DBH, volume stem⁻¹, volume ha⁻¹, volume year⁻¹, survival frequency of blanks (% 16 m² plots without living trees), number of stems ha⁻¹, number of undamaged stems ha⁻¹, basic density, tracheid length, diameter of thickest branch between one and two metres height, relative branch diameter (branch diameter in relation to stem diameter), number of branches whorl⁻¹ and branch angle.

| Trait | Transfer | | | | References |
|---|----------|-------|-------|-------|---------------------------|
| | 1.5° | 0° | -1.5° | -3° | |
| Height (m) | 8.7 | 8.6 | 8.3 | 7.7 | Persson and Ståhl 1993 |
| DBH (mm) | 129 | 125 | 120 | 113 | ibid. |
| Vol stem ⁻¹ (m ³) | 0.062 | 0.059 | 0.054 | 0.047 | ibid. |
| Vol ha (m ³) | 90 | 102 | 103 | 93 | ibid. |
| Vol ha year ⁻¹ (m ³) | 5.7 | 6.1 | 6.1 | 5.8 | ibid. |
| Survival (%) | 58 | 76 | 85 | 89 | ibid. |
| Blanks (% 16 m ²) | 10 | 0 | 0 | 0 | ibid. |
| Stems ha ⁻¹ (no) | 1190 | 1510 | 1730 | 1850 | ibid. |
| Undamaged stems ha ⁻¹ (no) | 230 | 370 | 500 | 630 | ibid. |
| Basic density (g cm ⁻³) | 0.32 | 0.33 | 0.34 | 0.34 | Ståhl 1988 |
| Tracheid length (mm) | 2.4 | 2.4 | 2.4 | 2.3 | ibid. |
| Thickest branch diam (mm) | 22.5 | 21 | 19.5 | 18.0 | Persson 1977, Remröd 1976 |
| Rel branch diam | 0.17 | 0.17 | 0.16 | 0.16 | Persson 1977, Remröd 1976 |
| No branches whorl ⁻¹ | 5.4 | 5.2 | 5.0 | 4.8 | Remröd 1976 |
| Branch angle (°) | 68 | 70 | 72 | 74 | ibid. |

provenances transferred southwards have a short shoot elongation period, in comparison to the local provenance (Langlet 1936, Hagner 1970, Ståhl 1984). These provenances have a high survival but a low stem wood production (Remröd 1976, Persson and Ståhl 1993, Persson 1994a, Persson 1994b). If these provenances will give a higher yield than that of the local material depends on the severity of the site. The short period of growth reduces the number of trees with spike knots and severe bends or other injuries (Ståhl et al. 1990). The short period of shoot elongation will leave time or temperature sum required for wood formation. Provenances transferred southwards will form thin annual rings, few and thin branches, little early wood, high basic density and slender tracheids with thick cell walls in comparison to local provenances (Ståhl and Ericson 1991).

In Table 2 yield and quality properties of alter-

native provenances in northern Sweden have been calculated. For a site at latitude 64°00' N 200 m.a.s.l. the calculated zero transfer was compared to a northwards transfer of 1.5° and a southwards transfer of 1.5° and 3°. The site would have a vegetation period of 150 days and a temperature sum (threshold temperature +5 °C) of less than 1000 day degrees (Perttu 1989). Survival, number of stems per hectare, frequency of blanks (16 m² circular plots without trees) height, DBH, volume/stem, and yield at an age of 27 to 29 years and predicted annual growth over a full rotation is compared for alternative provenance transfers. Looking at wood and stem properties, the number of undamaged stems/ha, wood density, tracheid length, branch diameter and relative branch diameter, furthermore number of branches per whorl and branch angle are calculated.

With a planting density of 2500 seedlings/ha

and comparing the two extreme transfers the volume production is similar but the average mean trees quite different. The trees of the material transferred northwards are larger but only one of five trees is undamaged. Basic density is comparably low and branches thick. With a three degrees southwards transfer we would have close to 1850 stems/ha and more than 600 trees without damage, basic density is comparably high, branches few and thin and with a fairly straight angle. Although differences would be smaller the same pattern can be seen between the local provenance and a material transferred 1.5° southwards. Thus, the choice of seed source has a large impact on the future use of the stand. A correct choice of seed source is an important first step in the silvicultural practise.

The policy of the land owner should be reflected in the seed source selection. For instance a private land owner aiming at producing high value saw timber and not wanting to spend much time and money into management should probably choose a northern material. Contradictory, a pulp and paper company with a short rotation intensive culture forestry in mind, may select a provenance of southern origin at least at some sites. An advantage with improving wood and stem properties through provenance choice is that it is inexpensive and fast in comparison to alternative breeding methods. It may be used with or without the cooperation of the silviculturist but the author would advocate for the integrated approach.

As an example the combination of retarded growth during one third of the rotation followed by increased growth (Fig. 1) may be achieved by using southern provenances in a narrow spacing and a gradual thinning. A northern provenance in a wide spacing would have the same diameter growth during the first part of the rotation but would have less growth potential during the late part of the rotation. However this is a hypothesis that still needs to be tested. Persson and Ståhl (1993) concluded that a narrow spacing would not influence volume production over the full rotation. Once a full crown closure is reached differences in stand density have little effect on stand productivity (Persson 1992). A crucial point in the hypothesis is if an increase in productivity achieved by provenance transfer corresponds to

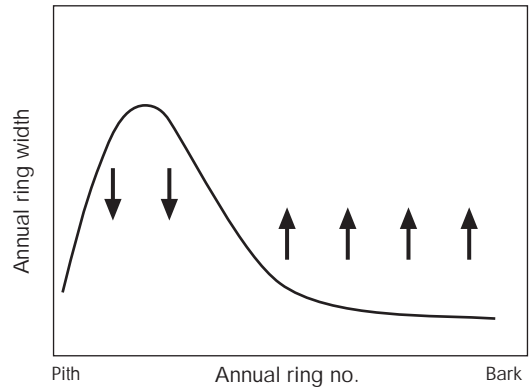


Fig. 1. Principal changes in annual ring width during a full rotation with conventional forestry and changes desired in order to improve wood properties.

an increase in site productivity, as argued by Persson and Ståhl (1993).

Another interesting approach where the provenance researcher may come in handy is the prognosis of future variation in wood and timber properties. Through use of national and international provenance trials the forest geneticist may separate geographical variation in wood properties from genetic effects and effects of silviculture. This has been done on the national level (review by Ståhl and Ericson 1991) but remains to be done internationally. In general, much is left to learn about the relations between growth phenology and wood formation at the genetic level. Although initial work has been done (Dietrichson 1964, Ericson et al. 1973, Antonova et al. 1983, Menyailo 1985) the effect on wood formation of genetic differences in growth phenology remains to be analysed. This must be done by evaluation of tracheid properties and wood variation within single annual rings and corresponding variation in weather conditions and phenology.

In forest genetics research we analyse the possibility to utilize existing differences in adaptive strategy within a species, to achieve seed sources suitable for future use in forestry. In order to meet the demands from sawmills, pulp and paper industry this must be done in cooperation among wood researchers, silviculturists and forest geneticists. A Scots pine breeding program

can only produce a good planting material. To manifest its full potential high quality seedling requires a good silvicultural treatment aiming at Scots pine stands with good wood and stem properties.

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References

- Andersson, B. 1986. Möjligheter till urval med avseende på virkeskvalitet i unga avkomme försök av tall. (Possibilities with selection for quality in young progeny trials of Scots pine (*Pinus sylvestris*)). Årsbok 1985, Föreningen skogsträdsfördling, institutet för skogsförbättring. p. 58–80. (In Swedish with English summary.)
- Antonova, G.F., Shebeko, V.V. & Malyutina, E.S. 1983. Sezonnaja dinamika kambialnoj aktivnosti i differentsiatsii trakheid v stvole sosny obyknovvennoj (Seasonal dynamics of cambial activity and tracheid differentiation in the stem of Scots pine). *Khimiya Drevesiny* No. 1. p. 16–22, 120. Sukachev Institute of Forestry and Timber, Krasnoyarsk, USSR.
- Boratynski, A. 1991. Range of natural distribution. In: Giertych, M. & Mátyás, C. (eds.). *Genetics of Scots pine*. Akademiai Kiado, Budapest. p. 19–30. ISBN 963-05-5891-2.
- Dickmann, D.I. 1985. The ideotype concept applied to forest trees. In: Cannell, M.G.R. & Jackson, J.E. (eds.). *Attributes of trees as crop plants*. Institute of Terrestrial Ecology, England. p. 89–101.
- Dietrichson, J. 1964. The provenance problem illustrated by studies of growth rhythm and climate. *Reports Norwegian Forest Research Institute* 19: 499–656.
- Donald, C.M. 1962. In search of yield. *Journal of the Australian Institute of Agricultural Science* 29: 171–178.
- Dormling, I. 1971. Photo- and thermoperiodische Reaktionen bei Fichte, Kiefer und Gerste. *Industrieller Pflanzenbau*, Band IX. p. 205–218. (In German.)
- Ericson, B., Johnson, T. & Persson, A. 1973. Ved och sulfatmassa från tall i örörda bestånd. (Wood and sulphate pulp of Scots pine from virgin stands). Royal College of Forestry, Department of Forest Yield Research, Research Notes 25. 143 p. (In Swedish with English summary.)
- Eriksson, G., Andersson, S., Eiche, V. & Persson, A. 1976. Variation between and within populations in a provenance trial of *Pinus sylvestris* at Nordanås, Lat. 64° 19', Long. 18 °09', Alt. 400 m. *Studia Forestalia Suecica* 133. 46 p.
- , Ilstedt, B., Nilsson, C. & Rytman, H. 1987. Within- and between-population variation of growth and stem quality in a 30-year-old *Pinus sylvestris* trial. *Scandinavian Journal of Forest Research* 2: 301–314.
- Eriksson, H. 1993. Ett modifierat trakthyggesbruk och virkesförsörjningen i framtiden. (A modified clear cutting system and future wood supply.) *Skogsakta Konferens* 17: 163–174. (In Swedish.)
- Giertych, M. 1991. Provenance variation in growth and phenology. In: Giertych, M. & Mátyás, C. (eds.). *Genetics of Scots pine*. Akademiai Kiado, Budapest. p. 87–101. ISBN 963-05-5891-2.
- Gullberg, U., Yazdani, R., Rudin, D. & Ryman, N. 1985. Allozyme variation in Scots pine (*Pinus sylvestris* L.) in Sweden. *Silvae Genetica* 34: 193–201.
- Hagner, M. 1970. An genecological investigation of the annual rhythm of *Pinus silvestris* L. *Studia Forestalia Suecica* 80. 40 p.
- Haygreen, J.G. & Bowyer, J.L. 1982. *Forest products and wood science – an introduction*. Iowa State University Press, Ames, Iowa. 500 p.
- Kärki, L. 1985. Crop tree ideotypes and harvest index should be the basis of selection in cultivated trees. *Foundation of Forest Tree Breeding in Finland, Annual report 1984*. p. 20–23.
- Koski, V. 1970. A study of pollen dispersal as a mechanism of gene flow in conifers. *Communicationes Instituti Forestalis Fenniae* 70(4). 78 p.
- 1985. Adaptation of trees to the variation in the length of the growing season. In: Kaurin, Å., Junttila, O. & Nilsen, J. (eds.). *Plant production in the north*. Norwegian University Press. p. 267–277.
- Langlet, O. 1936. Studier över tallens fysiologiska variabilitet och dess samband med klimatet. (Studien über die physiologische Variabilität und deren Zusammenhang mit dem Klima). 29. p. 219–470. (In Swedish with German summary.)

- 1959. A cline or not a cline – a question of Scots pine. *Silvae Genetica* 8: 13–22.
- Lindgren, O. 1991. The accuracy of medical CAT-scan images for non-destructive density measurements in small volume elements within solid wood. *Wood Science & Technology* 25: 425–432.
- , Davis, J., Wells, P. & Shadbold, P. 1992. Non-destructive wood density distribution measurements using computed tomography. *Holz als Roh- und Werkstoff* 50: 295–299.
- Menyialo, L.N. 1985. Role of the needles in hormonal regulation of zyllogenesis in pine. *Soviet Plant Physiology* 32: 95–100.
- Persson, A. 1976. Förbandets inverkan på tallens sågtimmerkvalitet (The influence of spacing on the quality of sawn timber from Scots pine). Royal College of Forestry, Department of Forest Yield Research, Research Notes 42. 122 p. (In Swedish with English summary.)
- 1977. Kvalitetsutveckling inom yngre förbandsförsök med tall. (Quality development in young spacing trials with Scots pine.) Royal College of Forestry, Department of Forest Yield Research, Research Notes 45. 152 p. (In Swedish with English summary.)
- Persson, B. 1994a. Effects of climate and provenance transfer on survival, production and stem quality of Scots pine (*Pinus sylvestris* L.) in northern Sweden. (Dissertation.) Swedish University of Agricultural Sciences, Department of Forest Yield Research, Report 37. 43 p.
- 1994b. Effects of provenance transfer on survival in nine experimental series with *Pinus sylvestris* (L.) in northern Sweden. *Scandinavian Journal of Forest Research* 9: 275–287.
- & Ståhl, E.G. 1993. Effects of provenance transfer in an experimental series of Scots pine (*Pinus sylvestris* L.) in northern Sweden. Swedish University of Agricultural Sciences, Department of Forest Yield Research, Report 35. 92 p. (In Swedish with English summary.)
- Persson, O. 1992. En produktionsmodell för tallskog i Sverige. (A growth simulator for Scots pine (*Pinus sylvestris* L.) in Sweden). Swedish University of Agricultural Sciences, Department of Forest Yield Research, Report 31. 206 p. (In Swedish with English summary.)
- Perttu, K. 1989. Climate in forestry – an introduction. In: MacIver, D.C., Street, R.B. & Auclair, A.N. (eds.). *Climate applications in forest renewal and forest production*. Canadian Government Publishing Centre, Ottawa, Canada. p. 19–25.
- Polge, H. 1963. Une nouvelle méthode de détermination de la texture du bois: L'analyse densitométrique de clichés radiographique. *Annales de l'Ecole Nationale des Eaux et Forêts de la Station de Recherches et Expériences* 20: 530–581.
- Pöykkö, T. 1993. Selection criteria in Scots pine breeding with special reference to ideotype. The Foundation for Forest Tree Breeding in Finland, Report 6. 66 p.
- Prescher, F. & Ståhl, E.G. 1986. The effect of provenance and spacing on stem straightness and number of spike knots of Scots pine in south and central Sweden. *Studia Forestalia Suecica* 172. 12 p.
- Prus-Glowacki, W. 1991. Biochemical polymorphism. In: Giertych, M. & Mátyás, C. (eds.). *Genetics of Scots pine*. Akademiai Kiado, Budapest. p. 73–86. ISBN 963-05-5891-2.
- Remröd, J. 1976. Choosing Scots pine (*Pinus sylvestris* L.) provenances in northern Sweden. Royal College of Forestry, Department of Forest Genetics, Research Notes 19. 132 p. (In Swedish with English summary.)
- Rendle, B.J. 1960. Juvenile and adult wood. *Journal of the Institute of Wood Science* 5: 58–61.
- Sarvas, R. 1974. Investigations on the annual cycle of development of forest trees. II. Autumn dormancy and winter dormancy. *Communicationes Instituti Forestalis Fenniae* 74(1). 101 p.
- Ståhl, E.G. 1984. Variation in shoot growth phenology among clones and populations of *Pinus sylvestris* L. (Dissertation.) Swedish University of Agricultural Sciences, Department of Forest Yield Research. 103 p. ISBN 91-576-1942-5.
- 1988. Transfer effect and variations in basic density and tracheid length of *Pinus sylvestris* L. populations. *Studia Forestalia Suecica* 180. 15 p.
- & Ericson, B. 1991. Inheritance of wood properties. In: Giertych, M. & Mátyás, C. (eds.). *Genetics of Scots pine*. Akademiai Kiado, Budapest. p. 231–241. ISBN 963-05-5891-2.
- & Persson, A. 1988. Wood quality and volume production in four 24-year-old provenance trials with *Pinus contorta*. *Studia Forestalia Suecica* 179. 20 p.
- Persson, A. & Persson, B. 1986. Timber quality in northern latitudes – implications for forest tree improvement. In: *Provenances and forest tree breeding for high latitudes*. Proceedings of the Frans Kempe Symposium in Umeå, June 10–11

1986. Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology. p. 149–158.
- Persson, B. & Prescher, F. 1990. Effects of provenances and spacing on stem straightness and number of stems with spike knots in *Pinus sylvestris* L. – Northern Sweden and countrywide models. *Studia Forestalia Suecica* 184. 16 p.
- Wilhelmsson, L. & Palmér, C-H. 1988. Skogsträdsförädling och tallkvalitet. Föreningen skogsträdsförädling, Institutet för Skogsförbättring, Årsbok 1987. p 38–45. (In Swedish.)
- Zimmerman, M.H. & Brown, C.L. 1971. *Trees: structure and function*. Springer, New York. 366 p.
- Zobel, B.J. & van Buijtenen, J.P. 1989. *Wood variation. Its causes and control*. Springer Verlag. 363 p.
- & Talbert, J. 1984. *Applied forest tree improvement*. John Wiley, Chichester. 505 p.

Total of 47 references