Silva Fennica 1991, Vol. 25 N:o 4: 207–214

Crown form and harvest increment in pendulous Norway spruce

Pertti Pulkkinen

TIIVISTELMÄ: RIIPPAKUUSEN LATVUSMUOTO JA MAANPÄÄLLISEN KASVUN JAKAANTUMINEN RUNKOON

Pulkkinen, P. 1991. Crown form and harvest increment in pendulous Norway spruce. Tiivistelmä: Riippakuusen latvusmuoto ja maanpäällisen kasvun jakaantuminen runkoon. Silva Fennica 25(4): 207–214.

Crown characteristics and the distribution of three years (1986–1988) biomass production of 20 pendulous Norway spruce (*Picea abies* f. *pendula* (Lawson) Sylvén) trees with heritable narrow crown and 15 normal-crowned (*Picea abies* (L.) Karst.) spruces were studied in a 19-year-old mixed stand. The form of the crown is conical in normal-crowned trees, columnar and narrow in pendulous trees. The partitioning of aboveground biomass to stems (Hinc) during studied 3 years was significantly higher in pendula (0.281) than in normal-crowned trees (0.255) and also the ratio between growth of stemwood and growth of needle biomass in studied three years was higher in pendula trees (0.67 g g^{-1}) than in normal crowned trees (0.52 g g^{-1}). The needle biomass in pendulous trees was distributed higher in the crown in pendula than in normal-crowned trees and they had a higher needle biomass/branchwood biomass ratio than normal trees. The difference in harvest increment between the two crown types are mostly due to the significantly lower branchwood biomass values in pendula than in normal-crowned trees. The higher needle 'efficiency' in pendula trees than in normal-crowned trees is probably connected with high partitioning of needle biomass to the upper part of the crown in pendula trees.

Normaalilatvuksellisten kuusten (*Picea abies* (L.) Karst) ja pendula-kuusten (*Picea abies* f. *pendula* (Lawson) Sylvén) tuottaman biomassan jakautumista sekä latvusominaisuuksia tutkittiin 19 vuotta vanhoista puista, jotka olivat kasvaneet samassa metsikössä. Normaalipuiden latvusmuoto on kartiomainen ja pendula-kuusien kapea sekä pylväsmainen. Pendula-kuuset allokoivat kolmen vuoden aikana tuottamastaan maanpäällisestä biomassasta merkitsevästi enemmän runkoon (0.281) kuin tavalliset kuuset (0.255). Myös pendula-puiden runkopuun kasvun sekä neulasmassan kasvun suhde tutkittuina kolmena vuotena oli korkeampi (0.67 g g^{-1}) kuin normaalilatvuksisten puiden (0.52 g g^{-1}). Pendula-puiden latvuksen yläosan neulasmassa on suhteellisesti suurempi kuin normaalilatvuksellisten puiden ja niiden neulasten massan suhde oksapuun massaan on suurempi. Ero tuotetun runkopuun osuuksissa maanpäällisen biomassan kasvusta tutkittujen puutyyppien välillä johtuu suurelta osin pendulapuiden merkitsevästi pienemmistä oksapuun massoista. Pendula-puiden normaalilatvuksellisia kuusia korkeampi neulasten 'tehokkuus' liittyy luultavasti pendula-puiden neulasten suureen määrään latvuksen yläosissa.

Keywords: crown, stems, biomass production, allocation, *Picea abies*, *Picea abies* f. *pendula*.
FDC 561

Author's address: Foundation for Forest Tree Breeding, Pieksämäki Nursery, Taimitarhantie 34, SF-76850 Pieksämäki, Finland.

Accepted February 14, 1992

1 Introduction

The crown form of the Norway spruce (*Picea abies* (L.) Karst.) is a variable character (Schmidt-Vogt 1986). However, a large part of the variation can be explained by the environmental factors (Schmidt-Vogt 1977) and the genetical determination of the crown form is obviously based on the polygenic system. The crown form of pendula spruce (*Picea abies* f. *pendula* (Lawson) Sylvén) is extremely narrow. The mean crown diameter of about 100-year-old trees with mean height of 25 meters was only 1.9 meters (Pulkkinen 1991a). This narrow crown form also inherited to 18–50% of open pollinated progenies, thus the inheritance of the crown form is based on only a few genes or gene groups (Lepistö 1985).

The form of the crown has been noticed to be an important factor determining the biomass production of the trees and it also affects allocation ratios between tree components (Cannell et al. 1983, Ford 1985, Pulkkinen 1991a, b). Also the crown structure has an effect on the stand factors (Jarvis et al. 1976, Mohler et al. 1978, Kellomäki et al. 1985, Pukkala and Kuuluvainen 1987), thus affecting also the stand stemwood production capacity.

At the individual tree level the stemwood production capacity can be characterized by using harvest increment values rather than harvest index values. The harvest increment is increment apportionable to the harvested part over a period of years within a lifespan of the trees (Cannell 1985). The harvest index is a measure for total lifespan of the trees, thus including several unknown factors of the history of trees and stands.

The objective of this study is to analyze relationships between crown form and stemwood production in heritable narrow crowned trees and in trees with normal crowns. The effect of crown characteristics and biomass partitioning on the wood production possibilities is also discussed.

2 Material and methods

The experimental trees were all open pollinated progeny of three pendula spruce trees growing in Mäntsälä, southern Finland. These Mäntsälä trees are characterized by thin and drooping branches, extremely narrow crown (Saarnijoki 1954, Pulkkinen 1991b) and the inheritance of the 'pendula-trait' (Lepistö 1985). Several hundreds of seedlings were grown in a nursery for 3 years and planted out in 1973 at a spacing of 2 × 2 m. The total study area was approximately 400 m² consisting 64 trees growing in four rows. All these trees were harvested in 1987 and 1988. However, only the trees felled in 1988 were measured with details and included in this study. The total number of trees felled in 1988 was 35 and consists 20 trees with pendula crown type and 15 trees with normal-crown type. The distinction between crown types was based on the differences in the diameter growth of the branches. This growth is almost totally arrested after second year in pendula trees (Pulkkinen 1991a).

Before the trees were felled in 1988, branch diameters were measured and sample branches were selected. Sample branches were the thickest, a medium and the thinnest living branch at whorl levels 1–4, 7 and 10. Branch angles and the distance between the tips of sample branches and the stem were recorded. The lengths of the sample branches and the positions of whorls were also recorded. Trees were divided into stem and crown, and the crown was further divided into crown layers, defined by means of whorls, which were numbered beginning from the top of the tree and included the branches in the whorl and corresponding interwhorl branches (interwhorl branches that arose in the same year as the whorl branches). Whorl branches were further divided into the annual amount of needles and corresponding amount of branch wood. All parts were weighed separately.

The dry weights of sample material were determined after drying at +105 °C for 48 h. The dry weights of crown components were estimated from the dry weights of needles and branch wood of sample branches. The stem was divided into seven sections above whorls 1, 2, 3, 4, 7 and 10 and the widths of the growth rings of each stems section was measured from the top and from the base of each section. The annual volumes of the stem sections were calculated from the diameters of the growth rings, and the total annual biomasses of stem wood was estimated by multiplying the annual volumes of stem sections by the density values of corresponding sections and summing the values obtained. The dry weight of stem bark was computed by multiplying volume of the bark by a density value of 0.365 (Kärkkäinen 1985).

Differences between crown types were studied by analysis of variance (Dixon et al. 1990). The equality tests of regression lines were carried out according to Dixon et al. (1990).

3 Results

Although the pendula spruces were taller than the normal-crowned spruces (Table 1), the mean maximal crown diameter was only 117 cm in pendula trees and 202 cm in normal-crowned trees (Table 1). Also the crowns had their maximal diameters more higher in pendula trees than in normal-crowned trees (Fig. 1a). The normal-crowned trees had thicker branches and smaller branch angles than pendula trees, but the branch lengths were quite similar in the two tree types (Table 1).

The mean values of all aboveground biomass components were higher in the normal-crowned trees than in the pendula trees (Table 1), and the differences were significant for needle and branchwood dry weights. There were no statistically significant correlations between tree height and needle biomass in the upper part of the trees in either crown type.

Maximal needle weight in normal-crowned trees was distributed little lower in the crown than in pendula trees (Fig. 1b,c). Within the upper part of the crown (layers 1–4, comprising 46% of the total height) normal-crowned trees carried 15% (601 g) and pendula trees 25% (635 g) of their total needle biomass ($p < 0.001$). The proportion of needles within the middle part of the crown (layers 5–7, 23% of the total height) was 42% (1707 g) in normal-crowned and 51% (1288 g) in pendula trees. Within the lower part of the crown (from layer 8 to the ground, 31% of total height) normal-crowned trees carried 43% (1776 g) of their total needle biomass, whereas pendula trees carried only 24% (593 g) ($p < 0.01$). When absolute biomasses were compared, differences between the two crown types were significant in the middle (t-test $p < 0.05$) and the lower parts of the crown ($p < 0.001$).

The allocation of branch biomass among crown layers of normal-crowned and pendulous trees was similar to that of needles. The ratios of

Table 1. Means and standard error of means of some morphological characters and biomass components (dry weight) of 19-year-old Norway spruce based on individual tree measurements (Pulkkinen 1991a).

Parameter	Crown form				t-test P-level
	Normal (n = 15)		Pendula (n = 20)		
	Mean	SE	Mean	SE	
Height, cm	428.1	25.5	471.2	18.6	NS
Maximal crown diameter, cm	202.4	9.5	116.7	5.4	< 0.001
Branch diameter, mm	11.2	0.4	8.6	0.3	< 0.001
Branch angle, °	74.4	2.1	99.0	1.9	< 0.001
Branch length, cm	69.2	2.3	63.7	3.2	NS
Needles, g	4083.8	397.9	2516.5	178.1	< 0.01
Branch wood, g	3457.4	361.6	1814.8	143.8	< 0.001
Stem, g	2783.3	379.6	2291.5	234.5	NS
Bark, g	323.6	42.9	262.9	29.0	NS

Table 2. Growth of aboveground biomass components during the 3 years period between 1986–1988 of 19-year-old Norway spruce based on individual tree measurements.

Parameter	Crown form: Normal (n = 15) Mean	SE	Pendula (n = 20) Mean	SE	t-test P-level
Needles, g	3682.7	353.7	2348.2	162.2	< 0.01
Branch wood, g	2820.3	297.8	1579.9	122.0	< 0.001
Stem, g	1915.5	276.5	1602.5	165.8	NS
Total, g	8418.5	854.3	5530.6	423.2	< 0.01

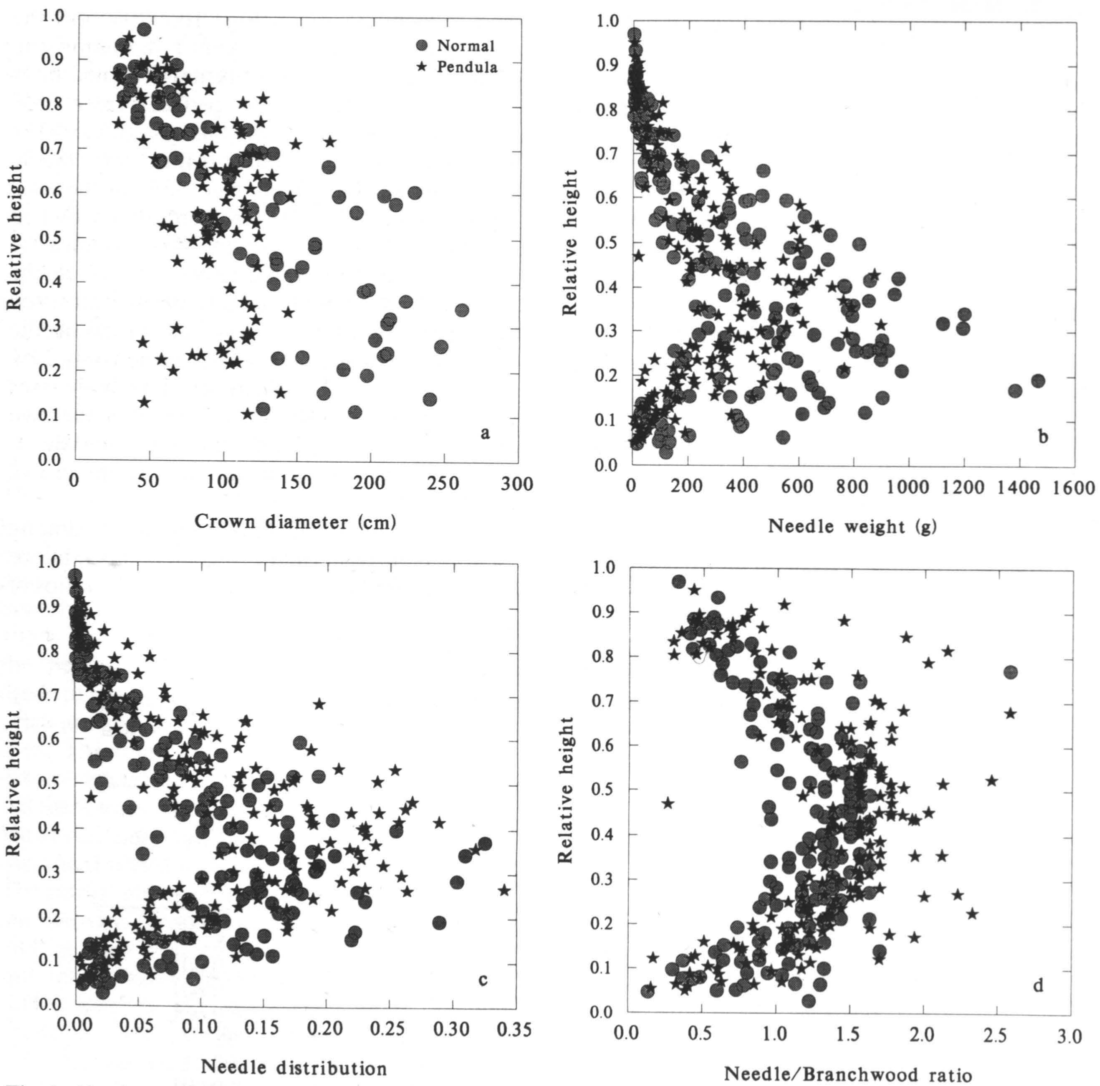

Fig. 1. Absolute values of crown diameters (a), needle biomasses (b), needle biomass distributions (c) and ratios between needle biomass and branch biomass (d) at different crown layers (whorl height/total height of the tree) in the normal-crowned and pendula spruces (symbols in Fig. 1a).

needle to branchwood biomass was significantly higher in pendula trees than in normal-crowned trees at upper and middle parts of the crown (Fig. 1d).

The production of aboveground biomass components and the allocation of biomass among needles, branch wood and stems (without bark) differed between crown types (Table 2). The

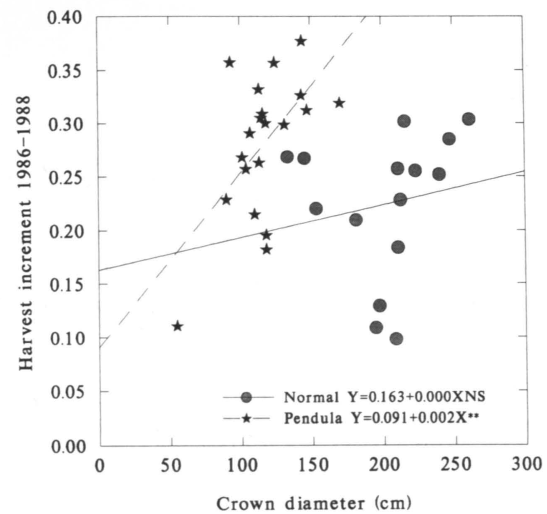

Fig. 2. Regressions of harvest increment (between 1986 and 1988) versus crown diameter in the normal-crowned and pendula spruces.

growth of needle and branch wood between studied three years were significantly higher in normal-crowned than in pendula trees, whereas growth of stemwood (without bark) was quite similar in normal-crowned and pendula trees.

Harvest increment (dry weight of stem growth without bark/dry weight of total aboveground growth between years 1986–1988) values were significantly higher ($p < 0.05$) in pendula (0.281) than in normal-crowned trees (0.225) and correlated significantly with crown diameter in pendula trees but not in normal crowned trees (Fig. 2). The growth of stem wood (without bark)/growth of needles (1986–1988) was 0.67 g g^{-1} in pendula and 0.52 g g^{-1} in normal-crowned trees ($p < 0.05$, Fig. 3a) and the corresponding ratios between branchwood and needles were 0.67 g g^{-1} and 0.76 g g^{-1} ($p < 0.001$), respectively (Fig. 3b). The aboveground harvest increment (1986–1988) showed positive correlation with the proportion of needle biomass to total biomass carried in the upper part of the crown in pendula trees, but not in normal-crowned trees (Fig. 4a), however the produced stem biomass (1986–1988) had no such correlation in neither crown types. Also the ratio between stemwood growth and needle biomass growth (1986–1988) increased significantly with increasing proportion of needle biomass (1986–1988) in the upper part of the crown in pendula trees, but not in the normal-crowned trees (Fig. 4b).

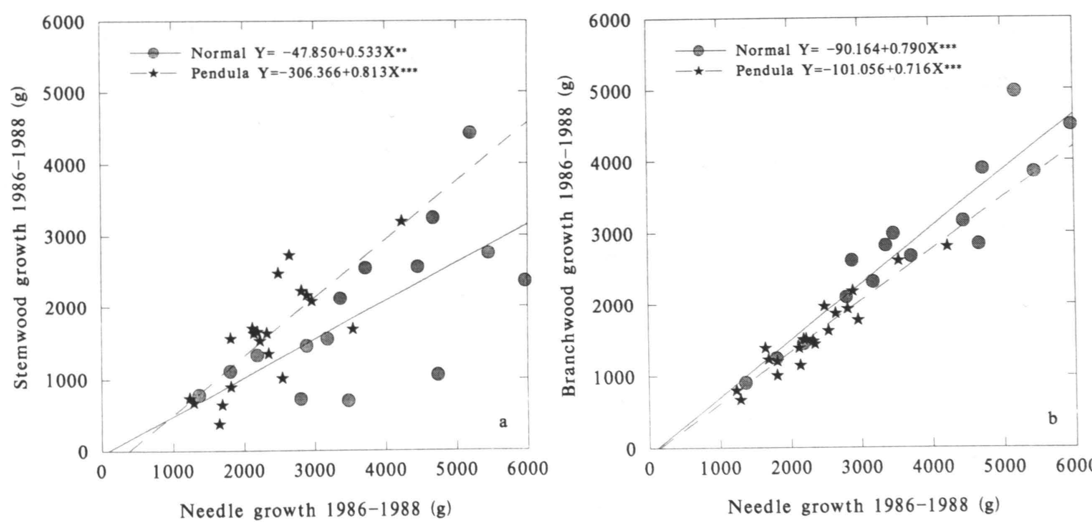

Fig. 3. Regression of stemwood growth (1986–1988, a) and regression of branchwood growth (1986–1988, b) versus growth of needle biomass (1986–1988) in the normal-crowned and pendula spruces.

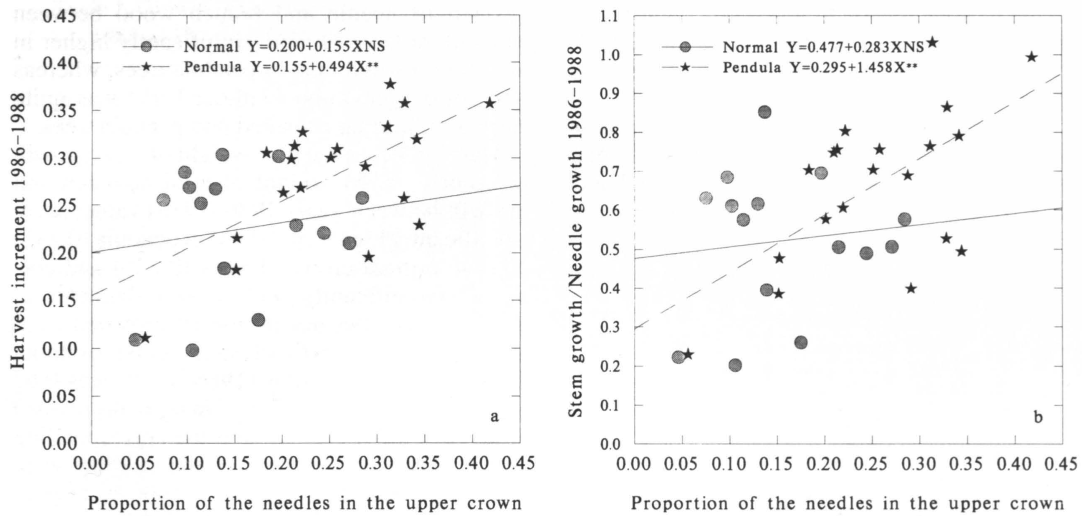

Fig. 4. Regression of harvest increment (1986–1988, a) and regression of stemwood growth/needle growth (1986–1988, b) versus proportion of the needles in the upper part of the crown (crown layers 1–4) to total needle biomass produced (between 1986 and 1988) in normal-crowned and pendula spruces.

4 Discussion

According to present results the narrow crowned spruces had higher allocation rates to stemwood than the normal-crowned trees. However, the total biomass per tree was smaller in pendula trees than in normal-crowned trees. The diameter of the crown in 19-year-old pendula trees was about the half of the diameter of normal-crowned trees and in over 100-year-old pendula trees the diameter still remained extremely narrow and showed no reaction to the free growth space (Pulkkinen 1991b). So it seems to be possible to increase the stocking density by using pendula trees at least if the crown characters are concerning. Also the form of the coarse-roots seems to be more narrow in pendula trees than in normal-crowned trees thus not preventing the idea of high stocking densities (Pulkkinen and Tigerstedt 1992).

Differences in biomass partitioning to the stem in normal-crowned and pendula trees is associated with crown structure, especially to the branch properties. The drooping form of branches in pendula trees is associated with arrested branch diameter growth after the second year (Pulkkinen 1991a). The difference in stemwood allocation ratios between pendula and normal crowned trees is almost totally explained by the higher branchwood ratio in normal crowned trees than in pendula trees. The branch structure of pendula trees had smaller supporting costs than the branches in normal crowned trees and hence had a surplus of assimilates. According to Cannell and Morgan (1990) the favorable structure for high production of surplus of assimilates might be a system of semi-pendulous shoots or shoots with high photosynthetic rates, a low level of annual shoot elongation and a high number of laterals.

The lower branchwood biomass, however, did not explain the differences betwe n pendula and normal crowned trees concerning produced stem biomass versus needle biomass. The production of stemwood/dry weight of needles was clearly higher in pendula than in normal-crowned trees. The proportion of needles distributed in the upper part of the crown was higher in pendula trees and in those trees the stemwood/needle ratio seems to be high. Also the ratio between stem biomass and needle biomass increased with needle biomass more rapidly in pendula than in normal trees (Pulkkinen and Pöykkö 1990, Pulkkinen 1991a). It is important to have the current-year and 1-year-old needles in conditions where shading is not a limiting factor for capturing radiation, because the rate of photosynthesis decreases with increasing age of the needles (Watts et al. 1976).

In dense stands the physical competition between pendulas might be small, but the production capacity of trees and stands are more depending on the efficiency of light interception than actual physical competition. The narrow-crowned coniferous trees in high latitudes had low within-tree shading (Kuuluvainen and Pukkala 1987). Shaded leaves in conifers are likely to be below the light compensation point for some of the time (Helms 1964). The addition of more leaves into the full shade of a closed canopy will not increase the production of photosynthates (McCree and Troughton 1966). In 19-year-old pendula trees the harvest increment values seem to increase with increasing proportion of needles located in upper crown. The high allocation rates to stem has been noticed in trees with narrow-crowns (Kellomäki 1986, Kuuluvainen 1991a). However, according to Kuuluvainen (1991b) a narrow and a long crown depicts increased between-tree shading at high latitudes, especially in dense stands.

References

Cannell, M.G.R. 1985. Dry matter partitioning in tree crops. In: Cannell, M.G.R. & Jackson, J.E. (eds.). Attributes of trees as crop plants. Inst. Terr. Ecol., Monks. Wood, Abbots Ripton, Hunts, U.K. p. 160–193.
— & Morgan, J. 1990. Theoretical study of variables affecting the export of assimilates from branches of Picea. Tree Physiol. 6: 257–266.
— , Sheppard, L.J., Ford, E.D. & Wilson, R.F.H. 1983. Clonal differences in dry matter distribution, wood specific gravity and foliage 'efficiency' in Picea sitchensis and Pinus contorta. Silvae Genet. 32: 195–202.
Dixon, W.J., Brown, M.B., Engelman, L. & Jennrich, R.I. 1990. BMDP statistical software manual. Vols. 1 and 2. Univ. California Press, Berkeley, Los Angeles, Oxford. 1385 p.
Ford, E.D. 1985. Branching, crown structure and the control of timber production. In: Cannell, M.R. G. & Jackson, J.E. (eds.). Attributes of trees as crop plants. Inst. Terr. Ecol., Monks. Wood, Abbots Ripton, Hunts, U.K. p. 228–252.
Helms, J.A. 1964. Apparent photosynthesis of Douglas-fir in relation to silvicultural treatment. For. Sci. 10: 432–442.
Jarvis, P.G., James, G.B. & Landsberg, J.J. 1976. Coniferous forest. In: Monteith J. L. (ed.). Vegetation and the atmosphere. Vol. 2. Academic Press, London. p. 171–270.
Kellomäki, S. 1986. A model for the relationship between branch number and biomass in Pinus sylvestris crowns and the effect of crown shape and stand density on branch and stem biomass. Scand. J. For. Res. 1: 455–473.
— , Oker-Blom, P. & Kuuluvainen, T. 1985. The effect of crown and canopy structure on light absorption and distribution in tree stand. In: Tigerstedt, P. M. A., Puttonen, P. & Koski, V. (eds.). Crop physiology of forest trees. Helsinki Univ. Press. p. 107–115.
Kuuluvainen, T. 1991a. Relationship between crown projected area and components of above-ground biomass in Norway spruce trees in even-aged stands: empirical results and their interpretation. For. Ecol. Manage. (in press).
— 1991b. Effect of crown and canopy architecture on radiation interception and productivity in coniferous trees. D. Sc. (Agr. and For.) thesis. Univ. of Joensuu. 25 p.
— & Pukkala, T. 1987. Effect of crown shape and tree distribution on the spatial distribution of shade. Agric. For. Meteorol. 40: 215–231.
Kärkkäinen, M. 1985. Puutiede. Sallisen Kustannus Oy, Sotkamo. 415 p.
Lepistö, M. 1985. Riippakuusen periytymisestä ja kapealatvaisuuden hyväksikäytöstä kuusen jalostuksessa. English summary: The inheritance of pendula spruce (P. abies f. pendula) and utilization of the narrow-crowned type in spruce breeding. The Foundation for Forest Tree Breeding, Information 1: 1–8.
McCree, K.J. & Troughton, J.H. 1966. Non-existence of an optimum leaf area index for the production rate of white clover under constant conditions. Plant Physiol. 41: 1615–1622.
Mohler, C.L., Marks, P.L. & Sprungel, D.G. 1978. Stand structure and allometry of trees during self-thinning of pure stands. J. Ecol. 66: 599–614.
Pukkala, T. & Kuuluvainen, T. 1987. Effect of canopy structure on the diurnal interception of direct solar radiation and photosynthesis in a tree stand. Silva Fenn. 21: 237–250.
Pulkkinen, P. 1991a. Crown structure and partitioning of aboveground biomass before competition phase in a mixed stand of normal crowned Norway spruce (Picea abies (L.) Karst.) and pendulous Norway spruce (Picea abies f. pendula (Lawson) Sylvén). Tree Physiol. 8: 361–370.
— 1991b. The pendulous form of Norway spruce as an option for crop tree breeding. Rep. Found.

Forest Tree Breed. 2: 1–30.
— & Pöykkö, T. 1990. Inherited narrow crown form, harvest index and stem biomass production in Norway spruce (Picea abies). Tree Physiol. 6: 381–391.
— & Tigerstedt, P.M.A. 1992. The form and mass of coarse-roots and root-shoot relationship in Picea abies and Picea abies f. pendula. Scand. J. For. Res. 7. In press.
Saarnijoki, S. 1954. Über ein Gruppenvorkommen von Trauerfichten, Picea abies (L.) Karst. f. pendula Jacq. & Hérincq. Commun. Inst. For. Fenn. 42. 42 p.
Schmidt-Vogt, H. 1977. Die Fichte. Ein Handbuch in Zwei Bänden. Band I. Taxonomie, Verbreitung, Morphologie, Ökologie, Waldgesellschaften. Paul Parey. Hamburg. 647 p.
— 1986. Die fichte. Ein Handbuch in Zwei Bänden. Band II/1. Wachstum, Zuchtung, Boden, Umwelt, Holz. Paul Parey. Hamburg. 563 p.
Watts, W.R., Neilson, R.E. & Jarvis, P.G. 1976. Photosynthesis in Sitka spruce (Picea sitchensis (Bong.) Carr.). VII. Measurements of stomatal conductance and $^{14}CO_2$ uptake in a forest canopy. J. Appl. Ecol. 13: 623–638.

Total of 25 references