Variation in Knot Size of *Pinus sylvestris* in Two Initial Spacing Trials

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The objective of this study was to investigate the variation in internal knot size of Scots pine (*Pinus sylvestris* L.) stems sampled from mature permanent plots, and for which the silvicultural history was known. It was based on a sample of mature trees removed from two different spacing trials representing a moderate and high site index. Knot size was measured with non-destructive methods using a CT-scanner and digital image analysis. Initial spacing varied between 0.75 and 3 m on the high site-index trial and between 1.5 and 2.5 m on the moderate site-index trial. Wider initial spacing on the high site index resulted in larger knots near the base of the stem. However, due to successive thinnings which gradually equalised stand density among plots, the difference between most plots was less further up in the stems. The effect of silvicultural regime was much more limited on the lower site index. Within-stand differentiation resulted in a variation of tree diameter (DBH); larger trees had significantly larger knots. Furthermore, knots were larger towards south than towards north in both trials. These results illustrated that, by using non-destructive measurements on trees sampled from permanent research plots, it was possible to simultaneously study the variation of internal knot size at stand (such as site and silviculture effects), within-stand (such as relative tree size) and within-tree levels (such as height and azimuth). However, lack of replication prevented valid statistical inference as to stand-level effects.

Keywords azimuth, initial spacing, knot size, silviculture, site quality, stand density, within-stand differentiation

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1 Introduction

The substantial effect of stand density on branch size has been reported by numerous authors for different coniferous species (Nylinder 1959, Grah 1961, Braastad 1970, Persson 1976, Persson 1977, Kenk and Unfried 1980, Abetz and Unfried 1983, Moltesen et al. 1985, Ballard and Long 1988, Skovsgaard 1988, Johansson 1992). These studies commonly pertain to single, stand-level effects primarily in the lower portions of the stems in order to make inference concerning wood quality aspects, and do not, for example, necessarily reflect the long-term dynamic implications of changing stand density levels over a whole rotation. Due to the lag in time between establishment of forest trials and merchantable maturity of the trees, it is often difficult to make inference concerning the impact of silvicultural practices on the quality of the final product in such studies (Nylinder 1959). This becomes even more evident when considering the ever-changing nature of ‘established’ silvicultural practices and end-user demands on forest products.

Methods that can be used to evaluate the dynamic effects of different silvicultural regimes using various simulation approaches have been presented for Scots pine (*Pinus sylvestris* L., Kärkkäinen 1986, Väisänen et al. 1989), Norway spruce (*Picea abies* (L.) Karst., Kärkkäinen 1986, Eriksson and Kyrkjeeide 1992, Houllier et al. 1995) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; Mitchell 1988, Maguire et al. 1991). These systems recursively employ branch and crown-recession models, together with mortality and individual tree growth models, in order to gradually simulate knot structure of individual trees. It is evident in these results that stand density, as affected by initial spacing and thinning, has a strong influence on tree growth, crown development and knot size. However, validation of these simulations is difficult because branch and knot data for the simulated silvicultural regimes are not usually readily available (Maguire et al. 1991). Furthermore, these model systems involve complicated error structures through the recursive use of linked models (Houllier et al. 1995). It is also difficult to translate (external) branch properties into (internal) knot structure (Taffe 1955), something which is a problem for the branch measurement methods presented above as well.

Stem dissection techniques have been developed to measure the internal, three-dimensional knot structure within stems (Koehler 1936, Maguire and Hann 1987, Johansson and Johansson 1988, Samson 1993). Recently, non-destructive methods have also been developed for internal stem measurements (Funt and Bryant 1987, Lindgren 1992, Grundberg 1994). These methods are time consuming (Oja 1997), but provide a means of directly observing quality traits within stems (such as knots) while also recognising the dynamic development of trees. Data obtained through application of such methods have been used to study geometric knot structure and past branch dynamics (Dietrich 1973, Kershaw et al. 1990, Maguire and Hann 1990, Björklund 1997, Lemieux et al. 1997). However, the impact of site and silviculture on knot structure is not directly analysed in these studies. Using such methods on stems sampled from permanent research plots, it would be possible to establish the connection between (past and present) growth conditions of trees and their internal knot structure. Moreover, it would be feasible to simultaneously study this relationship at several levels of variation.

Unfortunately, older forestry field trials in Sweden did not incorporate modern statistical techniques such as replication and randomisation (Eriksson 1986). Therefore, these trials cannot be used to make valid statistical inference as to stand-level effects. However, newer trials which include replication do not provide an opportunity to study the long-term effects of silvicultural treatments over a whole rotation till merchantable maturity. For the moment in Sweden (where rotation age can be 60–100 years or more), such studies are restricted to older trials, and the results must be viewed in light of the statistical limitations.

The objective of the work presented in this paper was to study the variation in internal knot size of Scots pine stems sampled from mature permanent plots, and for which the silvicultural history was known. The analyses were based on knot data obtained through non-destructive measurements (Grönlund et al. 1995) in order to describe several levels of variation, namely: between-stand variation; within-stand, between-tree variation; within-tree variation. Differences in knot size due to site quality, silvicultural regime, within-stand differentiation, height above ground and azimuthal direction (i.e. north-south orientation) were addressed. However, lack of replication prevented valid statistical inference as to stand-level effects.

2 Material and Methods

The study was based on a sample of 42 Scots pine trees removed in 1993 from permanent research plots within two different spacing trials (Granvik and Lycksele, Sweden). The trials were established at the beginning of the century, and lack replication. Initial spacing varied between 0.75 and 3 m on the high site index (S_h) and between 1.5 and 2.5 m on the moderate site index (S_m, see Table 1). There was thus a substantially larger spread in initial spacing within the former trial; narrow spacing was not well represented on the moderate site index.

Six trees representing three different diameter classes (two from each DBH-CLASS) were removed from each plot (Table 2). These classes represent the plot mean diameter (II) and classes separated by one half standard deviation below (I)

Table 1. Description of the research plots in the spacing trials.

Plot id	Location (latitude, longitude)	Site index (m)1)	Initial spacing (m)	Total age (yrs)	Plot mean DBH (cm)	Plot mean H_t2) (m)	Plot mean H_{llb}3) (m)
S_h0.75	58°39'N 14°34'E	28	0.75	87	30.8	25.6	16.2
S_h1.25	58°39'N 14°34'E	28	1.25	87	33.4	26.1	15.9
S_h1.5	58°39'N 14°34'E	28	1.5	87	34.0	26.1	15.4
S_h3	58°39'N 14°34'E	28	3	87	37.8	25.6	14.0
S_m1.5	64°41'N 18°43'E	24	1.5	76	20.3	19.0	9.5
S_m2	64°41'N 18°43'E	23	2	76	20.7	18.9	10.9
S_m2.5	64°41'N 18°43'E	23	2.5	76	19.8	18.7	9.5

1) SI defined as the dominant height at 100 years of age.
2) Total height.
3) Height to the lowest live branch.

Table 2. Description of the removed sample trees.

Plot id	DBH (cm) DBH-CLASS1)			$\overline{DBH}$	H_t (m) DBH-CLASS1)			$\overline{H}_t$	H_{llb} (m) DBH-CLASS1)			$\overline{H}_{llb}$
	I	II	III		I	II	III		I	II	III	
S_h0.75	26.4	29.2	34.6	30.1	25.2	26.7	26.6	26.2	16.2	16.2	17.6	16.6
S_h1.25	28.4	35.0	39.8	34.4	24.0	26.1	25.7	25.3	14.3	15.1	15.0	14.6
S_h1.5	28.0	34.2	40.4	34.1	22.3	27.3	27.0	25.5	13.3	17.6	14.1	14.9
S_h3	34.2	38.5	45.3	39.4	23.5	27.0	24.8	25.0	13.0	14.6	13.6	13.6
Mean	29.3	34.2	40.1	34.5	23.8	26.7	26.1	25.5	14.2	15.7	14.9	14.9
S_m1.5	19.2	22.4	25.8	22.4	18.8	19.7	20.0	19.5	9.6	11.1	11.0	10.6
S_m2	18.0	20.3	26.7	21.7	16.5	18.4	19.0	18.0	10.2	11.0	10.4	10.5
S_m2.5	19.5	23.0	25.7	22.8	18.0	18.2	19.9	18.8	9.5	9.8	11.2	10.0
Mean	18.8	22.0	26.1	22.3	17.8	18.8	19.7	18.7	9.7	10.6	10.7	10.4

1) Level II represents the stand mean DBH whereas I and III represent classes separated by one-half standard deviation below and above this value respectively.

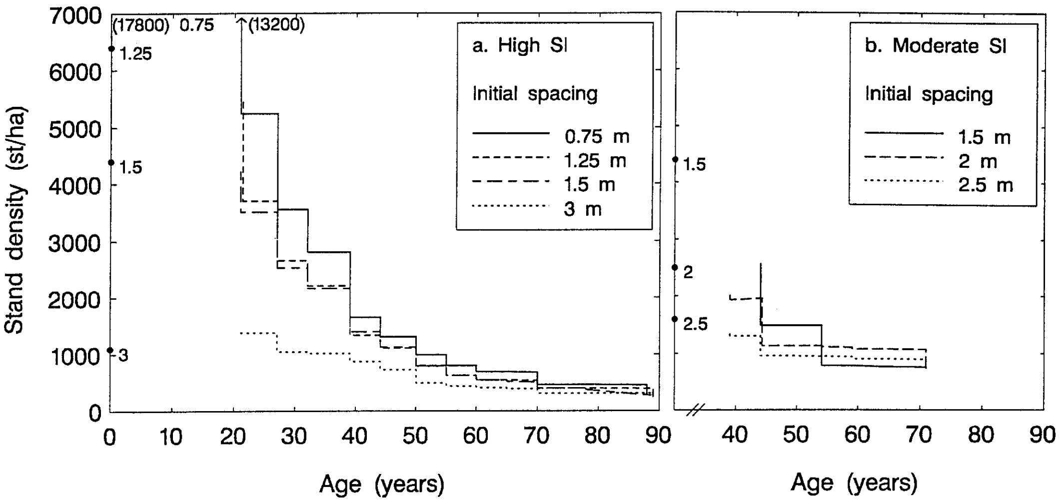

Fig. 1. Stand density development for S_h (a) and S_m (b). The dots (•) on the vertical axis denote the theoretical stand density at the time of planting.

and above this mean (III). They were quite narrow in the sense that very little diameter variation was allowed within each class (the mean difference in DBH between trees within pairs was about 1 cm). Within the respective plots, trees from the two largest diameter classes often had similar total heights, whereas the trees from the smallest diameter class were somewhat shorter. In fact, virtually all of the trees sampled represented the dominant crown class – largely due to the low level of stratification into crown classes present within the plots. The mean values of the sample trees (Table 2) seemed to correspond reasonably well to their respective mean plot values (Table 1).

The original aim of the trials at the time of planting early this century was not specifically to study knot size or other quality attributes, but rather to evaluate the effect of different silvicultural practices on total wood volume yield (see Maass 1910, Eklund 1956, Eriksson 1986). Different thinning schedules were applied in accordance with the experimental design for each trial. The stand density of the plots in the spacing trials was gradually reduced through successive thinnings so that, at the time of sampling, it was virtually equal for all plots within the respective trial (Fig. 1). In this paper, TREATMENT refers to the combined effect of the spacing and thinning regimes applied to each plot as presented in Fig. 1 and Table 1.

After field measurements, felling and cross-cutting, the logs were transported to a laboratory for CT-scanning and digital image analysis in order to study internal knot properties (sound-knot length, diameter and position within the stem for each knot, Grundberg 1994). Only the sawlog section of the stem (between stump level and the level where stem diameter over bark was 13 cm) was investigated.

The data was slightly unbalanced for the following reasons: the height of the top cross-cut was somewhat arbitrary since only the sawlog part of the stem was studied; some sub-sections did not contain any knots; some logs were missing due to severe damage or to becoming lost.

In this study, the diameter of knots at the sound/loose (intergrown/encased) knot border, defined as the maximum diameter of a knot in the transverse plane (Grönlund et al. 1995), has been evaluated. This corresponds to knot diameter at the time of branch death. The reason for this definition is that the resolution of the image is much higher in this plane with the measurement technology used. For the analyses, the data was divided into 1 m vertical stem-sections (HEIGHT LEVEL), and into 90° stem-quadrants (DIRECTION) according to azimuthal direction. KD_{max} refers to the diameter of the largest knot in each such sub-section. The following mixed model was fitted separately for S_h and S_m (although more interactions were tested, only those found significant are shown):

$$y_{ijklm} = \mu + A_i + B_j + C_k + D_l + (AC)_{ik} + (A\,B)_{ijm} + C\alpha(A\,B)_{ijkm} + D\alpha(A\,B)_{ijlm} + \varepsilon_{ijklm} \qquad (1)$$

where
y = KD_{max}
μ = intercept;
A = TREATMENT (stand level effect of silvicultural regime; see Fig. 1; fixed)
B = DBH-CLASS (within-stand tree size effect; j = I, II, III; fixed)
C = HEIGHT LEVEL (within-tree effect; See Fig. 2 for levels of k; fixed)
D = DIRECTION (within-tree effect of azimuth; l = N, E, S, W; fixed)
α = TREE (nested tree effect within A and B; m = 1–24 (S_h), 1–18 (S_m); random)
ε = residual error (random)

The results presented in this study were obtained with the SAS statistical package (version 6.12) using “Procedure Mixed” (see SAS Institute Inc. 1997). The means presented are the least square means. Unless otherwise stated, the significance levels in tests of equal means was $P < 0.05$. In pairwise comparison of main effect means, Tukey’s studentised test was used. The Restricted Maximum Likelihood (REML) method was used to estimate variance parameters. Various error structures within trees (including first order autoregressive, cf. Gregoire et al. 1995) and different bases for dividing stems into sections (see description above) were tested, but these efforts did not appreciably alter the results.

3 Results

The fixed effects – TREATMENT, DBH-CLASS, HEIGHT LEVEL and DIRECTION – were all found to be significant for S_h, the spacing trial on a high site index (Table 3). The only significant two-way interaction found was between TREATMENT and HEIGHT LEVEL. No higher order interactions were significant. As indicated in Fig. 2a, mean KD_{max} varied between about 21 and 31 mm in S_h; wider spacing resulted in larger knots (Fig. 2a). The difference between plots was most evident in the first stem section. At higher levels, the difference between treatments became much smaller. The differences at different HEIGHT LEVELs were especially large between the widest spacing (S_h3) and the others.

Knot size increased substantially from the lowest level (Fig. 2a), and seemed to reach a local maximum just above the base of the stem. Beyond this point, the plot with narrowest initial

Table 3. Variation of knot diameter (KD_{max}) within two initial spacing trials (1693 observations for S_h and 801 observations for S_m) with respect to TREATMENT, DBH-CLASS, HEIGHT LEVEL and DIRECTION.

Source of variation	NDF[1]	DDF[2]	F-value	Prob > F
High SI trial (S_h)				
TREATMENT	3	18	29.2	0.0001
DBH-CLASS	2	18	12.3	0.0004
HEIGHT LEVEL	19	326	7.5	0.0001
DIRECTION	3	69	19.1	0.0001
TREATMENT × HEIGHT LEVEL	57	326	2.9	0.0001
Moderate SI trial (S_m)				
DBH-CLASS	2	13	9.1	0.0034
HEIGHT LEVEL	13	146	9.7	0.0001
DIRECTION	3	51	6.2	0.0011

[1] Numerator degrees of freedom.
[2] Denominator degrees of freedom.

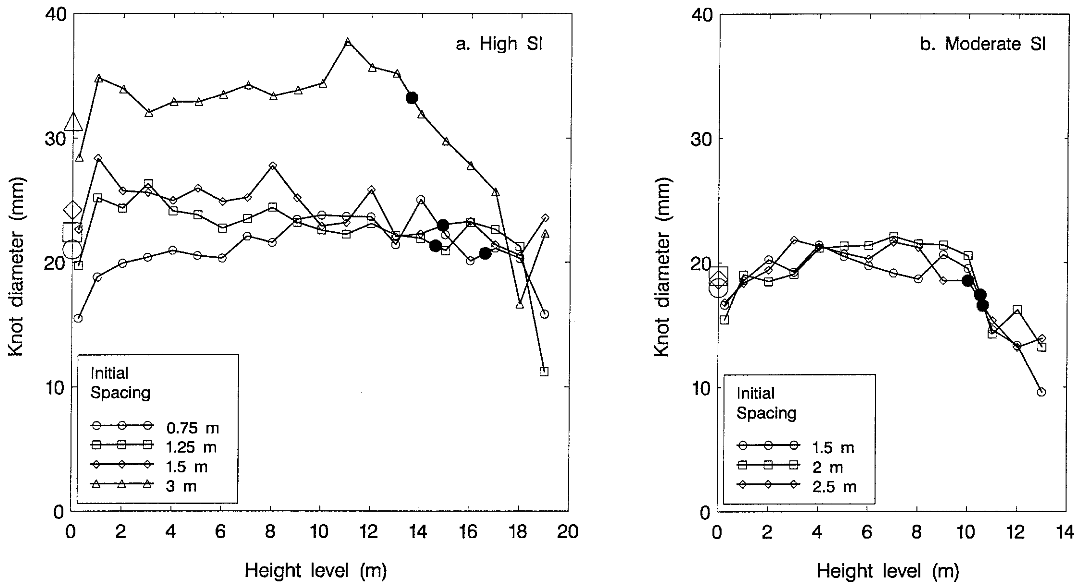

Fig. 2. Mean knot diameter (KD_{max}) for S_h (a) and S_m (b) pooled over all DBH-CLASSes and DIRECTIONs. Large symbols on the vertical axis are TREATMENT means. Dots (●) describe the vertical location of the first live branch (H_{llb}).

Table 4. Variance components (corresponding to Table 3) of the random effects for two initial spacing trials.

Source of variation	Variance Value	Variance %	Z-value	Prob > Z
High SI trial (S_h)	27.7	100		
TREE(TREATMENT DBH-CLASS)[1]	3.2	12	2.3	0.02
HEIGHT LEVEL × TREE(TREATMENT DBH-CLASS)	5.4	19	6.8	0.0001
DIRECTION × TREE(TREATMENT DBH-CLASS)	1.5	5	3.5	0.0004
Residual	17.6	64	24.5	0.0001
Moderate SI trial (S_m)	17.6	100		
TREE(TREATMENT DBH-CLASS)[1]	3.2	18	2.1	0.04
HEIGHT LEVEL × TREE(TREATMENT DBH-CLASS)	3.6	20	4.8	0.0001
DIRECTION × TREE(TREATMENT DBH-CLASS)	0.8	5	2.3	0.019
Residual	10.0	57	16.5	0.0001

[1] This denotes the nested, random TREE effect within TREATMENT and DBH-CLASS.

spacing (S_h0.75) indicated increased knot size with increasing height, whereas no such simple trend was evident for the other plots. The discrepancy in this development between plots contributed to the interaction effect observed in Table 3. Above the live crown, the plots had smaller knots with increasing height in the stem.

Virtually no differences in knot size were found between the plots in S_m (Fig. 2b). However, DBH-CLASS, HEIGHT LEVEL and DIRECTION were all found to be significant (Table 3).

Part of the sampling strategy was to select two trees from three different DBH-classes within each plot. The heterogenous diameter growth

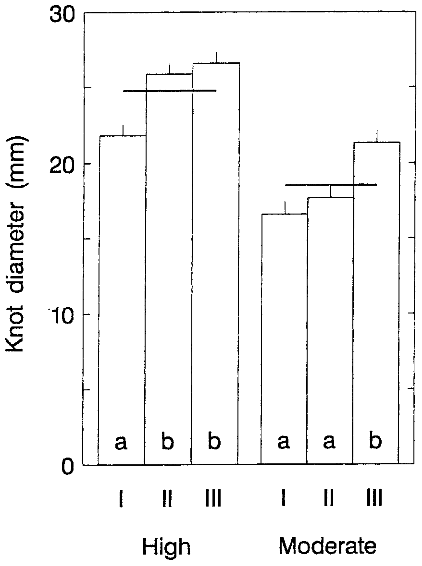

Fig. 3. Mean knot diameter (KD_{max}) of each DBH-CLASS pooled over all TREATMENTs, HEIGHT LEVELs and DIRECTIONs. I, II and III indicate DBH-CLASSes, 'high' and 'moderate' indicate site indices. DBH-CLASS means not having the same letter are significantly different ($P < 0.05$). Standard error is indicated by the vertical lines over the bars.

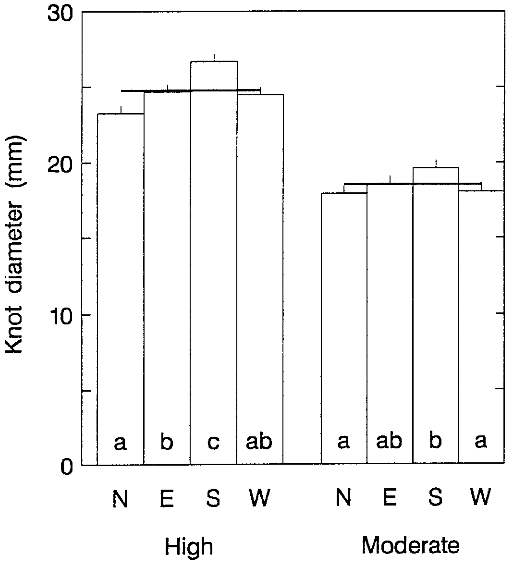

Fig. 4. Mean knot diameter (KD_{max}) in each DIRECTION pooled over all TREATMENTs, DBH-CLASSes and HEIGHT LEVELs. N, E, S and W indicate DIRECTIONs, 'high' and 'moderate' indicate site indices. DBH-CLASS means not having the same letter are significantly different ($P < 0.05$). Standard error is indicated by the vertical lines over the bars.

within the plots reflected some of the within-stand variation in knot size: DBH-CLASS was significant in both trials (Table 3); larger trees implied larger knots (Fig. 3). Variance associated with random tree-to-tree variation (within the TREATMENT/DBH-CLASS pairs) was found to be significant in both trials (Table 4), albeit of a smaller magnitude than the residual variance component.

The azimuth direction in which branches grew had a highly significant effect on knot size (Table 3). In general, the largest knots were found towards south, and the smallest knots were found towards north, while the other directions commonly resulted in intermediate knot sizes (Fig. 4). The effects of direction on knot size were similar for S_h and S_m, but, in comparison, the variation in absolute terms was somewhat smaller for the latter trial.

4 Discussion

4.1 Scope and Methodology

The experimental design of the spacing trials in this study was applied at the beginning of the century, and was not conducive for modern statistical evaluation of site or silvicultural treatment effects. The common experimental unit for such analyses is at the plot (or stand) level (Mead et al. 1993). However, replication in this study was only possible at the tree level. It was thus not possible to make any conclusive statistical inference regarding stand-level effects. Nevertheless, the results obtained in this study illustrated that, by using non-destructive measurements on trees sampled from permanent research plots, it was possible to simultaneously study the relationship between knot size and stand-level effects (such as site quality and silviculture), within-stand effects (such as relative tree size) and within-tree effects (such as height and azimuth). With an improved experimental and sampling design, more rigorous statistical methods could be applied, and stronger conclusions could be obtained.

Grönlund (1995) compares the CT-scanning method used in the present study (described by Grundberg 1994) with manual measurements on knots split through the centre for Scots pine. CT-scanning results in slightly larger knots; the mean difference is 5 mm. However, this is to be expected since the manual method has difficulty in locating the maximum knot diameter. Furthermore, there is no mean difference in the localisation of the dead-knot border – the point on the knot where diameter is measured (Grönlund 1995). Oja (1997) also compares the same non-destructive method with several manual, destructive methods for Norway spruce including stem dissection (e.g. Koehler 1936) and board measurements (e.g. Samson 1993). In terms of knot diameter, stem dissection is most precise, but is twice as time-consuming as the other two, and implies a systematic error due to difficulties in locating the knot centre. It would also be difficult to apply for Scots pine where many knots are occluded and difficult to identify from the outside. The standard deviation between CT-scanning and stem dissection for Norway spruce is 2.2 mm (Oja 1997). According to Oja (1997) CT-scanning is more precise than board measurements of knot size, while the time consumption of these two methods are similar.

The cross-section of Scots pine knots is oval (Lehtonen 1978). However, it is not possible to take this into account with CT-scanning due to the low longitudinal resolution. The CT-scanning method measures the horizontal diameter, whereas its vertical counterpart is about 4.3–8.5 % larger (Lehtonen 1978). On the other hand, it is difficult to obtain the true diameter with the manual methods discussed above, and it is therefore not apparent if there is a bias in the diameter measurement of Scots pine using CT-scanning. The low longitudinal resolution also implies that small knots (below about 10–12 mm) are difficult to detect and measure (Grönlund 1995, Oja 1997), but this should not be a large problem in the present study due the focus on large knots.

4.2 Between-Trial Variation

The different silvicultural regimes employed in each trial, the different stand ages, and the different locations (especially in terms of latitude, see Table 1) make it difficult to compare the two trials. The lack of replication prevents statistical inference of differences. Nevertheless, the plots in S_m resulted in smaller knots (Fig. 2b) in comparison with corresponding plots on the higher site index (S_h1.5 and S_h3 in Fig. 2a). This agrees with the well-established observation that trees growing on better sites, but with similar stand density conditions, will develop larger branches due to the larger foliage mass (Larson 1969, Uusvaara 1974, Turkia and Kellomäki 1987, Lämsä et al. 1990, Mäkinen and Uusvaara 1992).

The foliage mass and photosynthetic capacity of a stand has been found to be highly dependent on site factors such as nutrient availability (Brix 1971, Albrektson 1980, Axelsson 1984), water status (Grier and Running 1977, Linder and Axelsson 1982), and climate (Bergh et al. 1998). Better site conditions result in more foliage mass and greater photosynthetic capacity. Since there is a correlation between foliage mass and branch growth (Kellomäki 1980, Whitehead et al. 1990), it is not surprising that branches become larger in trees growing on better sites as was found when comparing Fig. 2a and 2b. Furthermore, Lämsä et al. (1990) observed that the longevity of branches is shorter on better sites. Madgwick et al. (1986) report that fertilised trees initially show higher branch growth rates (in terms of elongation) than control trees, but that the annual increment slows faster with branch age at a later stage. This latter (retardation) effect is attributed to the higher degree of inter-tree competition in the fertilised plots. The larger branches found on better sites can therefore be ascribed more to higher branch growth rates rather than longevity.

4.3 Between-Plot Variation

Due to successive thinnings, which started at a stand age of 21 years for S_h, it is likely that the effect of initial spacing is limited to the lower stem sections. Larger differences were found between plots in Fig. 2a near the stem base than higher up in the stems. By the time of sampling at 87 years of age, stand density (Fig. 1) and knot size (near H_{llb}, the solid dot in Fig. 2) were virtually equal among all plots. In fact, with the exception of the widest spacing, there were hardly any difference among plots above the 7 m HEIGHT LEVEL. Although it is difficult to compare (internal) knot data with (external) branch measurements (see Taffe 1955), these apparent stand density effects agree with earlier results concerning this trial (S_h). Based on measurements carried out when total stand age was 44 and 49 years, Persson (1976) found that branch diameter near breast height increases linearly with initial spacing, but that the difference between plots subsides with increasing height. Similar results have been reported in numerous other studies for different coniferous species (Cromer and Pawsey 1957, and Brown 1966, for *Pinus radiata* D. Don, Grah 1961, and Kenk and Unfried 1980 for Douglas-fir, Merkel 1967, and Moltesen et al. 1985 for Norway spruce; Godman and Cooley 1970 for *Pinus banksiana* Lamb.; Ballard and Long 1988 for *Pinus taeda* L.).

Diameter growth of branches in coniferous trees with strong apical dominance results in increasing branch basal diameter with increasing depth into the live crown from the stem apex down. The diameter reaches a maximum slightly above the base of the live crown (Colin and Houllier 1991, Colin and Houllier 1992, Maguire et al. 1994, Roeh and Maguire 1997) due to a period where branches survive without forming complete annual rings (Andrews and Gill 1939, Reukema 1959, Larson 1969, Kershaw et al. 1990, Weslien 1995). Stand density affects crown recession (Ritchie and Hann 1987, Maguire and Hann 1990) and thereby the length of the live crown (Kramer 1962, Arlinger 1996) through competition-induced branch mortality. The main effect of stand density on maximum attainable branch size, and on knot size (observed in Table 3 and Fig. 2), is thus through branch longevity and duration of radial growth (Kershaw et al. 1990).

On the poorer site (S_m), differences in knot size between plots were slight (Fig. 2b), both in terms of the mean values per plot (about 19 mm for all plots) and at individual HEIGHT LEVELs. This probably partially reflected the narrow range in initial spacing, and the effect of early mortality which further limited stand density differences as is evident when comparing stand density at the time of stand establishment and the first revision (38 years of age, see Fig. 1).

However, statistical evaluation of the TREATMENT effect in this study (Fig. 2) is made difficult due to the lack of stand-level replication. It is not possible to conclusively ascertain if differences in knot size were actually due to silvicultural regime, or to random differences in fertility and microclimate among plots, or to variations in spacing within plots due to early mortality and natural seeding, or to sampling deficiencies.

4.4 Within-Plot, Between-Tree Variation

As in the present study, a positive correlation between DBH and branch size has been found in many other studies (Cromer and Pawsey 1957, Elfving 1975, Persson 1977, Colin and Houllier 1992, Johansson 1992, Pukkala et al. 1992, Mäkinen 1996). Nylinder (1959) and Persson (1977) also identified an interaction effect of spacing and DBH on branch size based on earlier measurements within S_h. Similar results are indicated for Norway spruce by Johansson (1992). On the other hand, Cromer and Pawsey (1957), Moltesen et al. (1985) and Mäkinen (1996) did not find an interaction between stand density and DBH on branch size. Although DBH-CLASS was significant in the present study (Table 3), no interaction with TREATMENT was evident. Perhaps this was due to the numerous low thinnings that removed much of the heterogeneity within the plots, lack of stand-level replication or few number of trees sampled (i.e. 6 per plot).

Stem diameter growth is a relatively low priority sink of photosynthate allocation. It therefore follows that, as the growing space is redistributed among trees through within-stand differentiation (see Mitchell 1975, Oliver and Larson 1990), smaller crowns – as well as smaller branches – are associated with smaller trees in terms of DBH and vice versa. However, the repeated thinnings applied in the trials (Fig. 1) have limited the extent of differentiation evident within the plots, and reduced the potential effect of tree size in comparison with the possible result of within-stand differentiation under a no-thinning regime.

4.5 Vertical Within-Tree Variation

Björklund (1997) studied the internal knot structure of Scots pine trees, and identified different vertical knot sections. Although the effects of silviculture or site properties on the variation in knot size are not addressed, an hypothesis is presented concerning the vertical variation of maximum knot diameter. An initial increase in knot size above the butt of the stem, corresponding to Björklund's (1997) establishment section, was evident for all plots (except one, $S_m1.5$) in Fig. 2a and 2b. Given the correlation between branch size and foliage mass (Kellomäki 1980, Whitehead 1990, Gilmore and Seymore 1997), it is likely that this development is related to the initial accumulation of foliage in a stand (Long and Smith 1984). Branches near the stem base were probably affected by competing subordinate vegetation such as shrubs as well (Mitchell 1975).

As a result of natural thinning in a fully stocked even-aged stand, it has been suggested that the growing space, and the foliar biomass, is redistributed so that an equilibrium level of foliage is maintained (Long and Smith 1984). Under such conditions, crown extension of the dominant trees would proceed as suppressed trees become overtopped (Mitchell 1975, Oliver and Larson 1990), and knot size of the residual trees would be expected to increase with increasing height above ground (Maguire et al. 1994). As a result of thinnings, this development would occur in intervals (Maguire et al. 1991), corresponding to height of the crown base at the time of the removal. Although it was not possible to directly link the removal of trees through thinnings to knot size at any particular height level in the present study, there did not seem to be any systematic pattern in vertical knot size development between the initial increase during establishment and the decrease above the live crown (discussed below). Knot size increased for $S_h0.75$ (in Fig. 2a, as was discussed above), while it remained more or less level for most other plots in this middle section. Björklund (1997) also describes a stem section above 2.5 m height whereby knot size remained reasonably constant, and suggests that this is due to a period of high height growth and constant rate of crown recession. All plots indicated local maxima within this middle stem section, which could be evidence of thinning responses. But, it is not possible to make conclusive inference on the nature of this relationship on the basis of this data.

Branch diameter decreased above the lowest live branch (the solid dot in Fig. 2a and 2b), which is in accordance with Björklund's (1997) crown section. This is to be expected due to the decreasing branch age with increasing height into the live crown (Kershaw et al. 1990, Colin and Houllier 1991, Maguire et al. 1994), although only the lower part of the live crown was represented in this study. The results became uncertain in the uppermost HEIGHT LEVEL due to the few number of observations.

4.6 Azimuthal Within-Tree Variation

Very few results are available in the literature concerning the azimuthal variation in either knot or branch size. Lemieux et al. (1997) studied the knot geometry in different directions, and found the largest knot volume towards southeast. But, since these sectors also had the largest number of knots, it is not clear what influence azimuth has on knot diameter. Significant differences with respect to azimuth have been found for sapwood content (Yang et al. 1985) – a property which, like branch growth, is also related to foliage mass (Kaufman and Troendle 1981). It is likely that the azimuthal variation is related to light intensity and its effect on the rate of net photosynthesis, both of which have been found to be greatest towards the south (Kunstle and Mitscherlich 1977, Troeng and Linder 1981, Kellomäki and Strandman 1995). This implies higher branch growth rates towards the south, and could explain the larger knots found in this direction (Fig. 4).

As spacing trials, great care was taken in obtaining a uniform spatial distribution of the seedlings at the time of establishment. In a situation where the trees are clustered to a greater extent, azimuthal effects on knot size would be more dependent on heterogenous competition between trees than on north-south orientation (cf. Stiell 1982). However, in order to get a better understanding of the azimuthal variation in knot size, further analysis on a broader material is necessary.

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