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Effect of provenance and spacing on stem straightness and number of stems with spike knots in *Pinus sylvestris* L. – Northern Sweden and countrywide models

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Abstract

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Nine Scots pine (*Pinus sylvestris* L.) trials, situated north of latitude 61°N, were studied. The frequency of trees with straight stems and one or more spike knots was evaluated at a tree age of 27–29 years. A model was developed describing geographical variation, and was based on 19 provenance trials from different parts of Sweden. North of latitude 61°N, an average of 30 per cent of the stems were straight enough to produce a first-class bottom log of sawtimber. In addition, 47 per cent of the trees had no spike knots up to 5 m height. Significant variation between provenances was found in stem straightness and spike knot frequency in most trials. Provenances transferred southwards were straighter and had fewer spike knots than the corresponding local provenance. The frequencies and numbers of straight stems and trees without spike knots were higher at 1.25 m spacing than at 2.0 m spacing. The general models for geographical variation indicate that the highest number of straight stems without spike knots may be found between latitudes 58° and 65°N and at altitudes below 250 m.

Key words: *Pinus sylvestris* L., provenance, spacing, stem straightness, spike knot, Northern Sweden.

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Introduction

In Scots pine (*Pinus sylvestris* L.) the value of a tree depends on the quality of the timber, mainly the quality of the bottom log. Unfortunately, in Sweden, the quality of pine timber is decreasing, mainly owing to silvicultural methods used in reforestation and stand treatment (Persson, 1983).

Forest tree breeding may be one way of breaking this negative trend, although its results will not be realized in the near future. In a combined population-progeny trial, Eriksson, Ilstedt, Nilsson & Rytman (1987) assessed ca 25 quality characters, and found significant differences between populations for most of them. Within-population differences were significant in some cases. Clonal variation in stem straightness and frequency of spike knots was found by Andersson & Hattemer (1978) and Lindgren (1985). According to Pöykkö (1982) and Velling (1982) the heritability of quality characters is approximately 40–50 per cent, which indicates that breeding for quality is possible.

Besides branch diameter and basic density, the main factors affecting timber quality are stem straightness and the frequency of spike knots. Bends affect the volume of sawn goods and can, if severe, cause reaction wood to be formed. Spike knots decrease the strength of sawn products, especially when combined with ingrown bark. Both bends and spike knots can be caused by the loss of leading shoots as a result of harsh climate. Thus, a high frequency of bends and spike knots could be expected in northern Sweden, even though other quality traits are enhanced by the slow volume increment in this region (Ståhl, Persson & Persson, 1986). Consequently, by

selecting a hardy reforestation material, the frequency of spike knots and bends might be reduced. Prescher & Ståhl (1986) concluded that although slow-growing provenances have a relatively lower frequency of trees with spike knots and bends than fast-growing provenances, within a given provenance the tallest trees were the least affected. This relationship suggests that trees with spike knots and bends are also affected by growth-inhibiting damage.

Gullberg & Vegerfors (1987) reported results from spacing trials with Scots pine in southern and central Sweden. The results show that as spacing increases, so does the frequency of spike knots. Similar results were found by Prescher & Ståhl (1986), who reported that in southern and central Sweden a change in spacing from 2.0 m to 1.25 m corresponds to a 2° southward provenance transfer. In addition, as spacing is reduced, branch number and branch diameter decrease (Oker-Blom, Kellomäki, Valtonen & Väisänen, 1988; Kellomäki & Tuimala, 1981; Persson, 1976, 1977; Huuri & Lähde, 1985).

The objectives of this study are (1) to describe the influence of provenance and spacing on stem straightness and number of trees with spike knots for Scots pine in northern Sweden and (2) to formulate a generalized countrywide model for describing the effects of geographical origin on these two quality traits.

The study is based on a series of trials, of which the southern trials were earlier analysed by Prescher & Ståhl (1986). This makes it possible to compare the present results with those of the previous study.

Material and methods

Material

The material used for this study is part of the large-scale Scots pine provenance series planted in Sweden during the period 1952–1955 (Eiche, 1966). In this series 29 trials are situated between latitudes 56° and 68°N and at altitudes from 5 to 765 m above sea level. Nine of the northern trials are included in the present

study. A total of 44 provenances was analysed. Table 1 gives the latitude, longitude and altitude of trials and lists the provenances in each trial. Figure 1 shows the distribution of trial sites and origins of the provenances.

Table 1. Description of trial locations and list of provenances included in each trial

Trial No.	Site	Latitude °N	Longitude °E	Altitude m.a.s.l	Provenances
11	Högståsen	61°05'	14°58'	365	10, 21, 33, 40, 42, 49, 51, 53, 56, 58, 72, 74, 82, 85
14	Brämön	62°12'	17°41'	15	21, 23, 25, 34, 36
15	Vallbogården	63°10'	13°06'	525	2, 10, 23, 25, 34, 36, 37, 38, 39, 42, 50, 74, 107, 110
18	Robertsfors	64°10'	20°52'	40	10, 23, 26, 42, 74, 102, 103
19	Harrsjön	64°15'	15°20'	350	4, 10, 23, 26, 42, 50, 106
20	Storberget	64°34'	18°15'	455	5, 10, 11, 13, 19, 23, 28, 32, 42, 43, 55, 101, 106, 108
21	Långsjöby	65°09'	16°34'	470	4, 10, 23, 26, 38, 102, 108
22	Asplövberg	65°39'	21°07'	60	5, 10, 11, 20, 23, 34, 47
25	Ohtanajärvi	66°56'	23°11'	200	3, 4, 10, 11, 13, 19, 23, 26, 36, 42, 50, 74, 101, 103

Each trial includes 7 or 14 provenances. The experimental design is an incomplete latin square, also called a Youden square (Cochran & Cox, 1957), with seven treatments, replicated four times. Although the trials with 14 provenances are not true Youden squares, their randomization and restrictions are based on the same assumptions. In each trial, two of the four blocks have a 2.0 m×2.0 m spacing, while

the other two have a 1.25 m×1.25 m spacing. Each plot contains 50 and 80 trees at the wide and narrow spacing, respectively.

The time elapsed since planting varied between 27 and 29 years, depending on the year of establishment and on the years of assessment. Precommercial thinnings were carried out once in most of the trials, in either 1968 or 1975.

Methods

Field measurement

The variables measured were height, diameter at breast height (dbh), bark thickness, height to first live branch, stem straightness and number of spike knots. Stem straightness from ground level to 5 m height was graded using the following five classes related to sawtimber quality:

- 1 = totally straight stem
- 2 = minor bend
- 3 = bend or bends affecting final timber quality
- 4 = severe bend or bends, resulting in poor timber quality
- 5 = not useful for sawtimber because of bends.

This classification was made subjectively by the same experienced person in all trials.

The number of spike knots was counted between ground level and 5 m above ground. Because the most valuable sawtimber is obtained from the lower section of the trunk, this part only of the trunk was evaluated. Trees were divided into five classes:

- 0 = no spike knots
- 1 = one spike knot
- 2 = two spike knots
- 3 = three spike knots
- 4 = four or more spike knots.

In the analysis, only trees taller than 4 m were included, to avoid bias in estimates caused by differences in tree height.

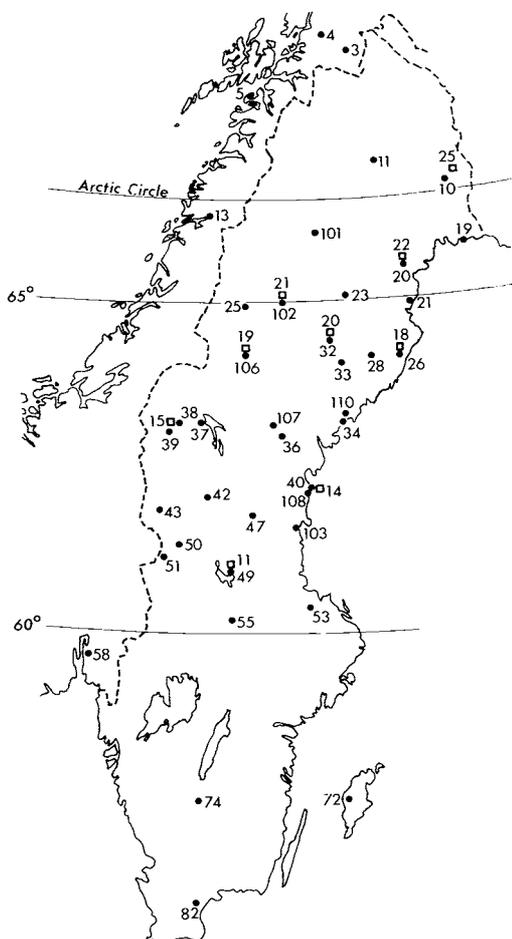


Fig. 1. Locations of trials (□) and provenances used (●).

Computations

To discern differences in stem straightness and frequency of spike knots between provenances, χ^2 analysis was used.

Due to the fact that the χ^2 test is a large-sample approximation, and because the number of observations in some classes was low, classes were pooled to ensure that the smallest expectation was at least 1 in any class, as recommended by Snedecor & Cochran (1967). Combinations differed depending on the plantation site (Table 2).

Two kinds of correlation were calculated separately for each trial: Correlations based on provenance mean values, and partial correlations based on single-tree values with provenance differences eliminated.

The numbers of straight stems (class 1+2) and stems without spike knots (class 0) per hectare were calculated for both narrow and wide spacings. The influence of latitudinal transfer at different spacings on the characters studied was analysed using linear regression.

To formulate a generalized countrywide model describing the variation in stem straightness and spike knot frequency, data from Prescher & Ståhl (1986) were included. The analysis was based on a method developed by Campbell (1974) and Eriksson, Andersson, Eiche, Ifver & Persson (1980). As a first step the local provenance value was calculated for each spacing and trial by means of stepwise multiple regression analysis. The regression function used was

$$Y = a + b_1 \Delta lat + b_2 \Delta alt + b_3 \Delta lat^2 + b_4 \Delta alt^2 + b_5 \Delta lat \cdot \Delta alt$$

where

Y = number of straight stems per hectare or numbers of stems without spike knots,

Δlat = latitudinal transfer in decimal degrees (negative values indicate southward transfer),

Δalt = altitudinal transfer in metres (negative values indicate downward transfer).

The intercepts of the regression functions were used as estimates of the local provenance values. In a second step, the geographical variations in numbers per hectare of trees without spike knots and trees with straight stems, were analysed. The estimated local provenance values were included as dependent variables in the following stepwise regression model:

$$Y_o = a + b_1 lat + b_2 alt + b_3 lat^2 + b_4 alt^2 + b_5 lat \cdot alt + b_6 sp + b_7 sp \cdot lat + b_8 sp \cdot lat^2 + b_9 sp \cdot alt + b_{10} sp \cdot lat \cdot alt$$

where

Y_o = estimated value per hectare of the numbers of straight stems or trees without spike knots,

lat = latitude of the trial in decimal degrees,

alt = altitude of the trial in metres,

sp = indicator variable for spacing (1.25 m = 1, 2.0 m = 0).

In the functions presented, only variables significant at the 5 per cent level were included.

Table 2. Number of classes in χ^2 analyses and corresponding degrees of freedom

Trial No.	Frequency of spike knots		Stem straightness	
	No. of classes	Degrees of freedom	No. of classes	Degrees of freedom
11	3	26	4	39
14	3	12	5	24
15	5	52	3	26
18	3	12	4	18
19	4	18	4	18
20	3	24	3	24
21	3	12	3	12
22	4	18	4	18
25	4	30	3	18

Results

Table 3 shows the numbers and percentages of stems without spike knots (spike knot class 0) and straight stems (stem straightness class per trial 1+2). Mean values for height and volume per stem are also shown.

In Fig. 2 assessments of spike knot frequency are shown separately by provenance. Trial mean percentages are given, as are levels of significance between provenances. Corresponding values for stem straight-

ness are given in Fig. 3.

The degrees to which spike knot frequency and stem straightness are correlated with height, diameter and stem volume are presented for each trial. In Table 4 correlations are based on provenance mean values, while in Table 5 they are based on single-tree values after elimination of provenance differences. Number of spike knots and stem straightness are related to spacing at each site in Tables 6 and 7.

Table 3. Numbers and percentages of trees without spike knots (class 0) and trees with straight stems (class 1+2) mean height and volume per stem for each of the trials

Trial No.	Spike knot class 0		Stem straightness class 1+2		Height (m)	Volume/stem (dm ³)
	No. of trees	%	No. of trees	%		
11	898	69	545	43	10.2	76
14	664	84	293	37	10.3	81
15	476	18	515	51	3.6	7
18	677	70	354	37	9.0	55
19	264	40	80	14	7.4	45
20	617	41	451	32	6.1	30
21	309	48	126	20	6.9	41
22	322	39	100	12	8.5	54
25	184	17	223	22	6.4	29
Mean		47		30		

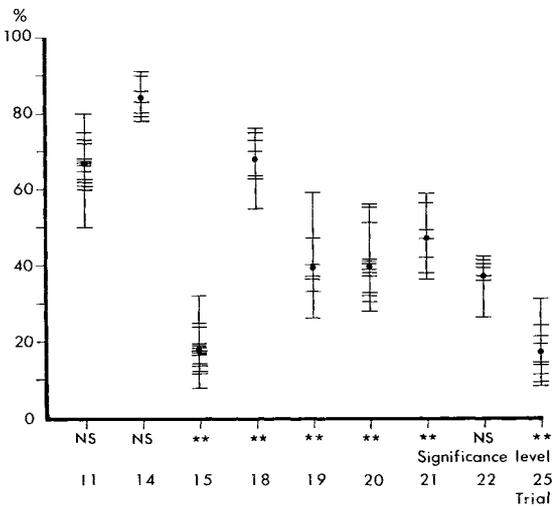


Fig. 2. Percentage of trees without spike knots (class 0) for each provenance (–) and trial (●). Significance levels based on χ^2 analysis.

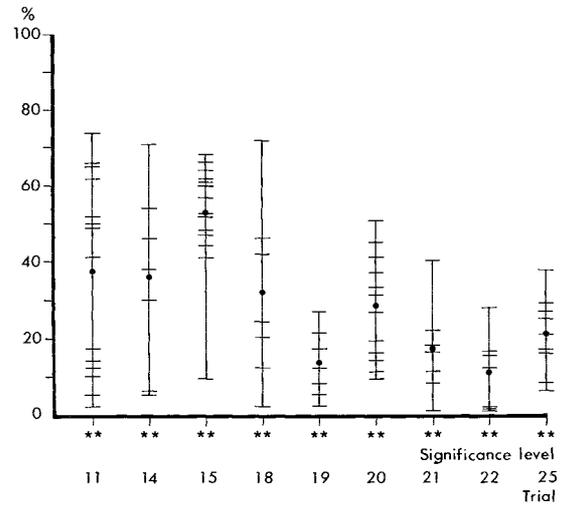


Fig. 3. Percentage of trees with straight stems (class 1+2) for each provenance (–) and trial (●). Significance levels as in Figure 2.

ns = not significant at 1 per cent level

** = significant at 1 per cent level.

Table 4. Correlation coefficients between different variables, based on provenance means

Trial No.	No. of spike knots		Volume/ stem	Stem straightness		Volume/ stem	No. spike knots
	DBH	Height		DBH	Height		
11	.188 ^{ns}	.069 ^{ns}	.209 ^{ns}	.702 ^{**}	.565 [*]	.678 ^{**}	.557 [*]
14	.242 ^{ns}	.170 ^{ns}	.260 ^{ns}	.628 ^{ns}	.870 [*]	.678 ^{ns}	.139 ^{ns}
15	.225 ^{ns}	.162 ^{ns}	.199 ^{ns}	-.144 ^{ns}	-.225 ^{ns}	-.070 ^{ns}	.641 [*]
18	.668 ^{ns}	.246 ^{ns}	.587 ^{ns}	.903 ^{**}	.542 ^{ns}	.847 ^{ns}	.858 [*]
19	.710 ^{ns}	.800 [*]	.706 ^{ns}	.758 ^{**}	.832 [*]	.725 ^{ns}	.898 ^{**}
20	.396 ^{ns}	.032 ^{ns}	.301 ^{ns}	-.222 ^{ns}	-.600 [*]	-.288 ^{ns}	.646 [*]
21	.694 ^{ns}	.617 ^{ns}	.685 ^{ns}	.444 ^{ns}	.375 ^{ns}	.444 ^{ns}	.923 ^{***}
22	.572 ^{ns}	-.097 ^{ns}	.417 ^{ns}	-.147 ^{ns}	-.427 ^{ns}	.013 ^{ns}	.775 [*]
25	.624 [*]	-.199 ^{ns}	.466 ^{ns}	.744 ^{**}	-.247 ^{ns}	.633 [*]	.825 ^{***}

^{ns} = not significant at the 5 per cent level

^{*} = significant at the 5 per cent level

^{**} = significant at the 1 per cent level

^{***} = significant at the 0.1 per cent level

Table 5. Partial correlation coefficients between different variables based on individual tree values. Provenance differences eliminated

Trial No.	No. of spike knots		Volume/ stem	Stem straightness		Volume/ stem	No. spike knots
	DBH	Height		DBH	Height		
11	-.257 ^{***}	-.320 ^{***}	-.243 ^{***}	-.210 ^{***}	-.328 ^{***}	-.205 ^{***}	.554 ^{***}
14	.038 ^{ns}	-.050 ^{ns}	.041 ^{ns}	.100 ^{ns}	.004 ^{ns}	.109 ^{**}	.427 ^{***}
15	.122 ^{***}	.047 [*]	.087 ^{***}	.009 ^{ns}	-.094 ^{***}	-.009 ^{ns}	.092 ^{***}
18	-.074 [*]	-.166 ^{***}	-.079 [*]	.090 ^{**}	.009 ^{ns}	.101 ^{**}	.349 ^{***}
19	-.051 ^{ns}	-.133 ^{***}	-.121 ^{**}	-.030 ^{ns}	-.103 ^{**}	-.070 ^{ns}	.064 ^{ns}
20	-.036 ^{ns}	-.122 ^{***}	-.043 ^{ns}	-.023	-.085 ^{**}	-.031 ^{ns}	.283 ^{***}
21	.013	-.111 ^{**}	-.018 ^{ns}	.153 ^{***}	.038 ^{ns}	.130 ^{ns}	.428 ^{***}
22	-.070 [*]	-.146 ^{***}	-.082 [*]	-.013 ^{ns}	-.158 ^{***}	-.034 ^{ns}	.351 ^{***}
25	-.016 ^{ns}	-.176 ^{***}	-.048 ^{ns}	.061 [*]	-.093 ^{**}	.055 ^{ns}	.285 ^{***}

^{ns} = not significant at the 5 per cent level

^{*} = significant at the 5 per cent level

^{**} = significant at the 1 per cent level

^{***} = significant at the 0.1 per cent level

Table 6. Percentages and numbers of trees per hectare without spike knots for each of the trials, as relate spacing

Trial No.	Trees without spike knots (class 0)			
	% Spacing, m		No. of stems/ha Spacing, m	
	1.25	2.0	1.25	2.0
11	76	64	1080	925
14	92	79	1655	1335
15	20	16	870	305
18	72	67	2010	1160
19	44	33	1070	275
20	41	42	860	565
21	56	39	1125	400
22	39	39	925	570
25	16	19	245	175
Mean	51	44	1095	634

Table 7. Percentages and numbers of trees with straight stems (class 1+2) per hectare, as related to spacing for each of the trials

Trial No.	Trees with straight stems (class 1+2)			
	% Spacing, m		No. of stems/ha Spacing, m	
	1.25	2.0	1.25	2.0
11	52	37	675	515
14	46	31	820	530
15	47	48	745	455
18	39	34	1075	595
19	13	11	310	95
20	29	34	580	440
21	23	16	460	160
22	13	11	320	155
25	26	17	380	160
Mean	32	27	595	345

Fig. 4 shows the effect of provenance transfer on the number of spike knots for each trial and spacing. The results can be used to calculate the latitudinal provenance transfer necessary to meet various minimum requirements with regard to numbers per hectare of stems without spike knots in northern Sweden. Corresponding values for stem straightness are presented in Fig. 5.

The calculated numbers of stems without spike knots per hectare for the local provenance in different parts of Sweden at 2.0 m and 1.25 m spacings are presented in Fig. 6. The calculated numbers of straight stems at 2.0 m and 1.25 m spacings are presented in Fig. 7.

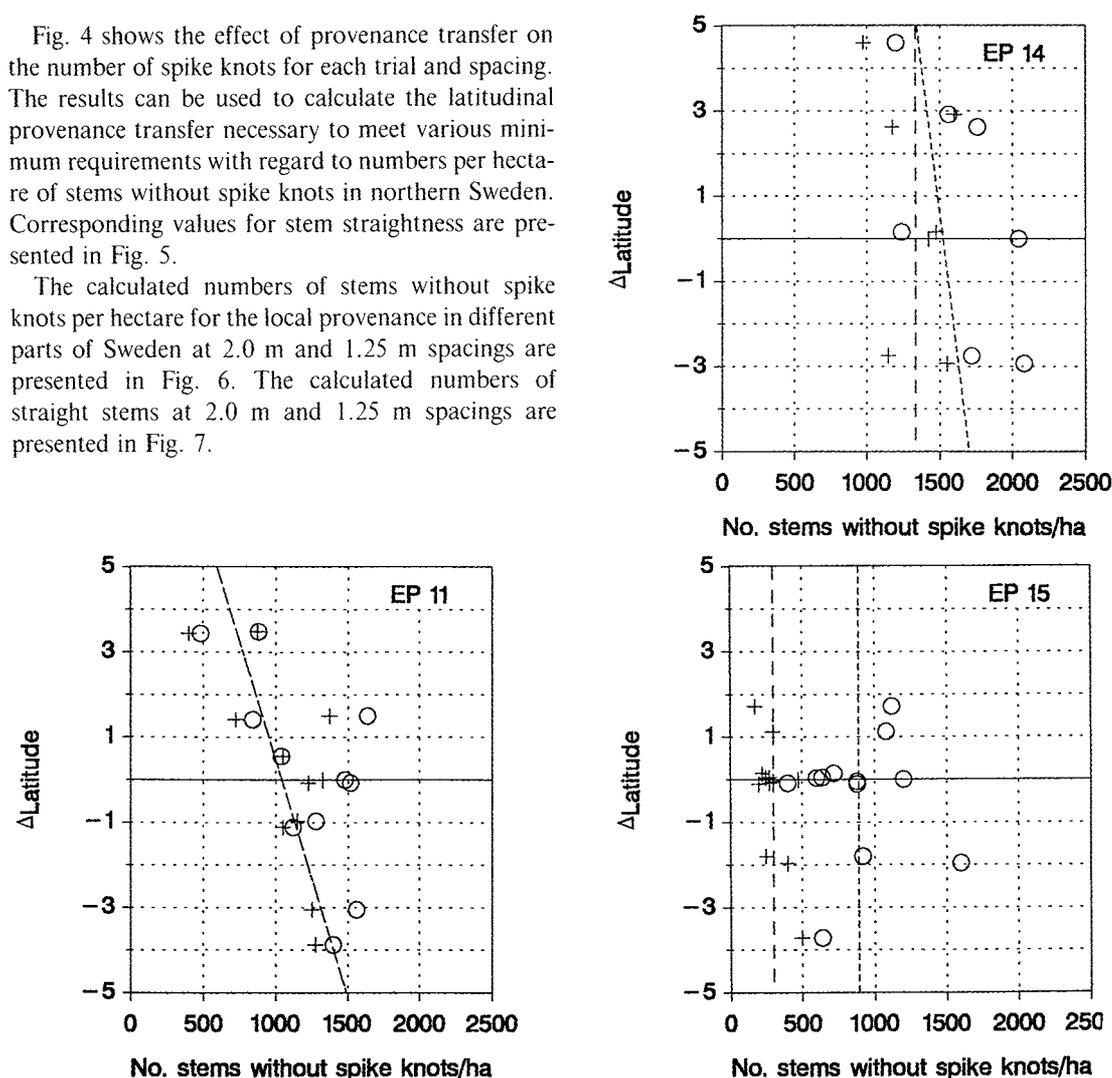


Fig. 4. Effects of latitudinal transfer on the number of trees without spike knots per hectare at 1.25x1.25 m (--- and O) 2.0x2.0 m (— and +) spacings for each provenance. A positive value for latitudinal transfer corresponds to a northy displacement.

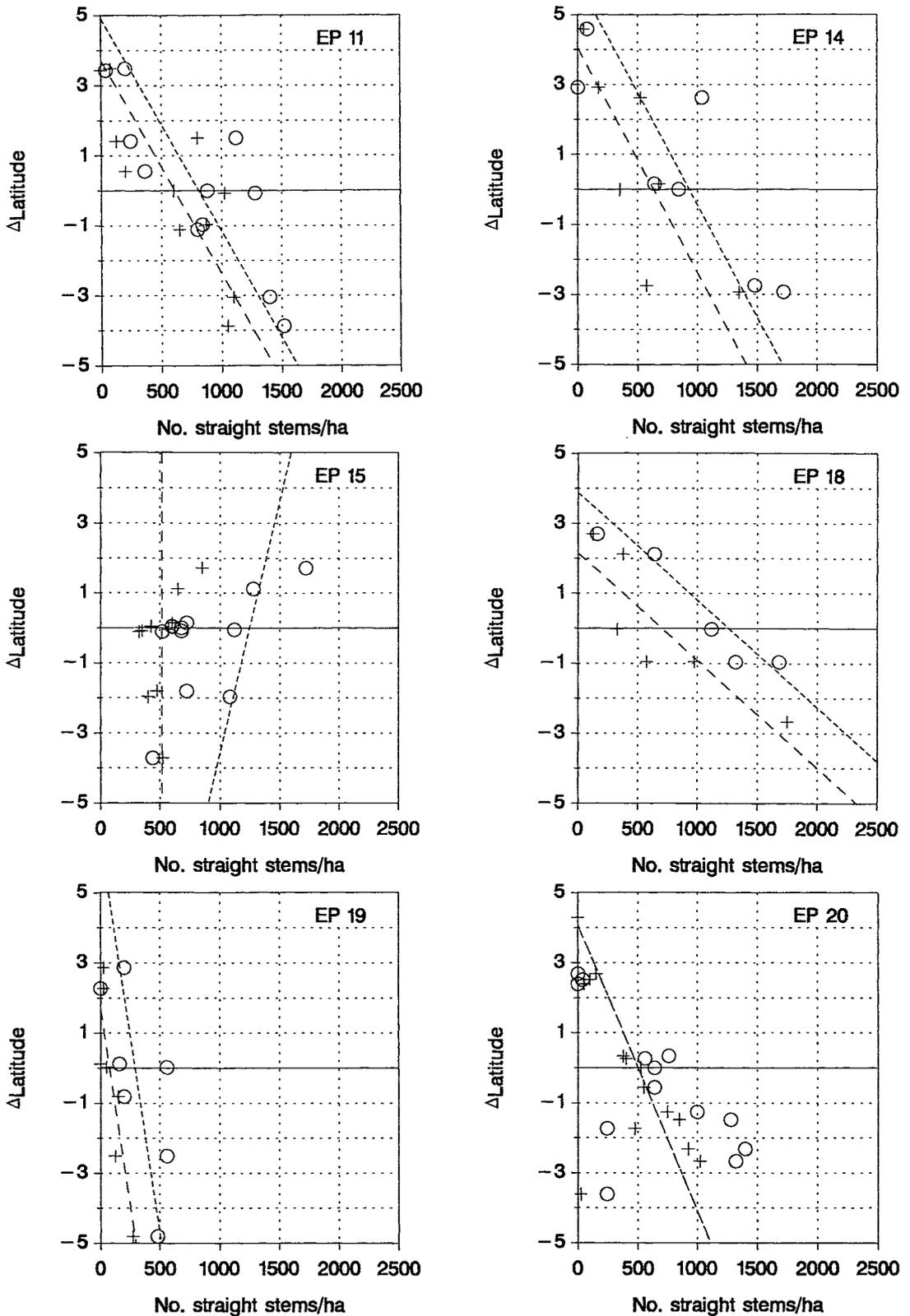
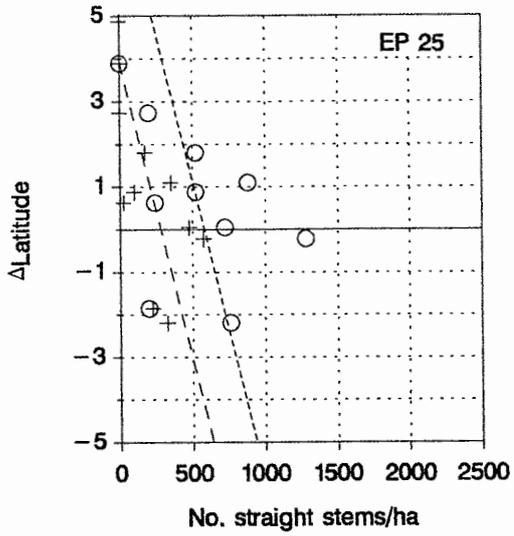
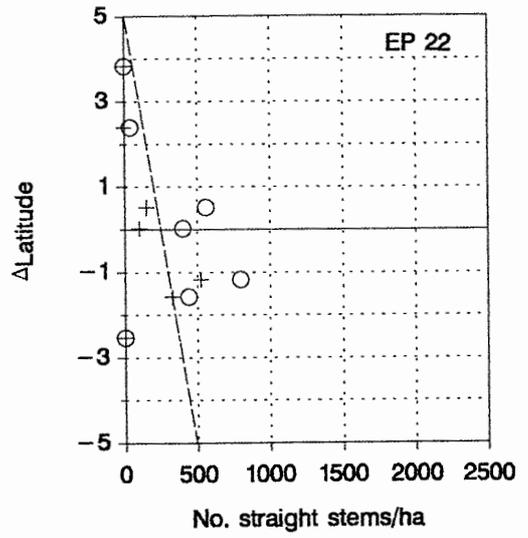
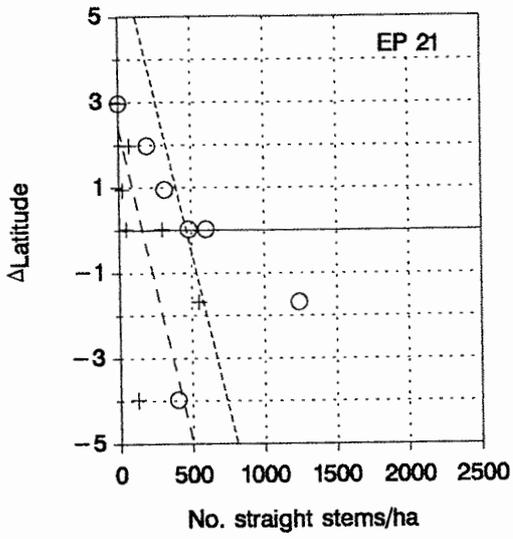


Fig. 5. Effects of latitudinal transfer on the number of trees with straight stems per hectare at 1.25x1.25 m (--- and O) and 2.0x2.0 m (---- and +) spacings for each provenance. A positive value for latitudinal transfer corresponds to a northward displacement.



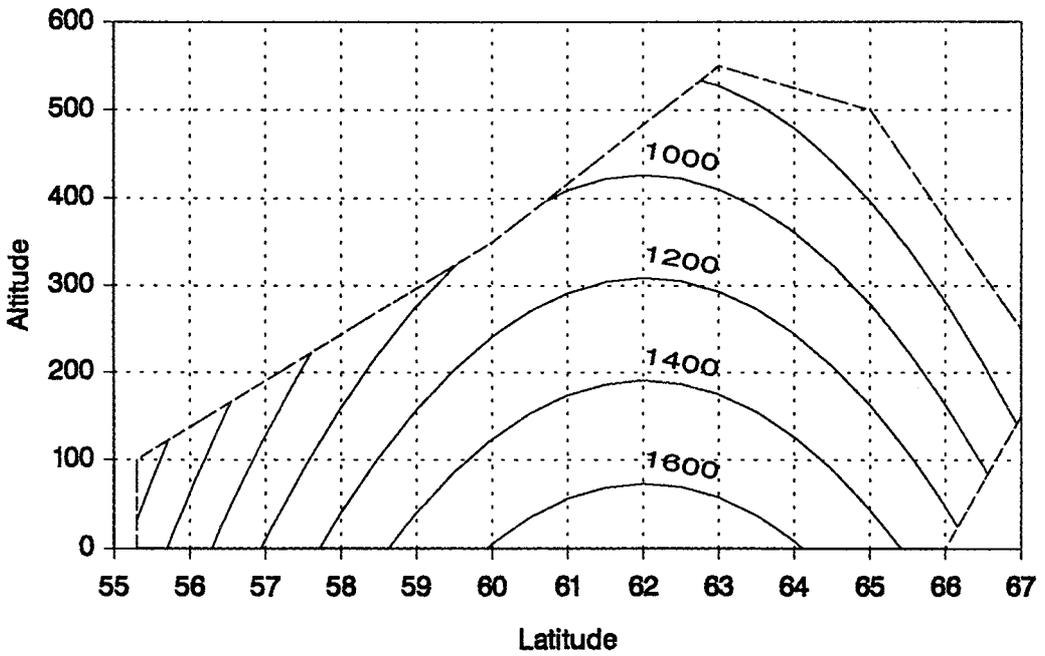
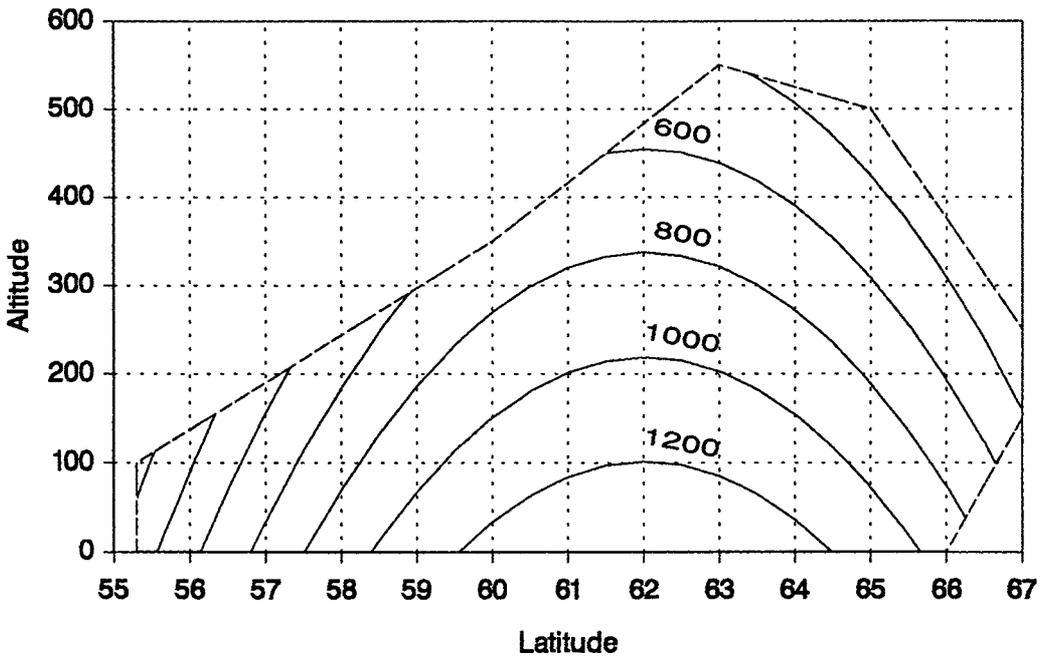


Fig. 6. Model predicting locally the number of stems per hectare without spike knots (SWS) at 2.0 m (A) and 1.25 m (B) spacings.

$$SWS = 1003 + 352 \cdot sp + 57.35 (lat-61)^2 - 28.08 (lat-61) - 1.628 (alt-200)$$

$$R^2 = 0.56 \quad S_{y \cdot x} = 361$$

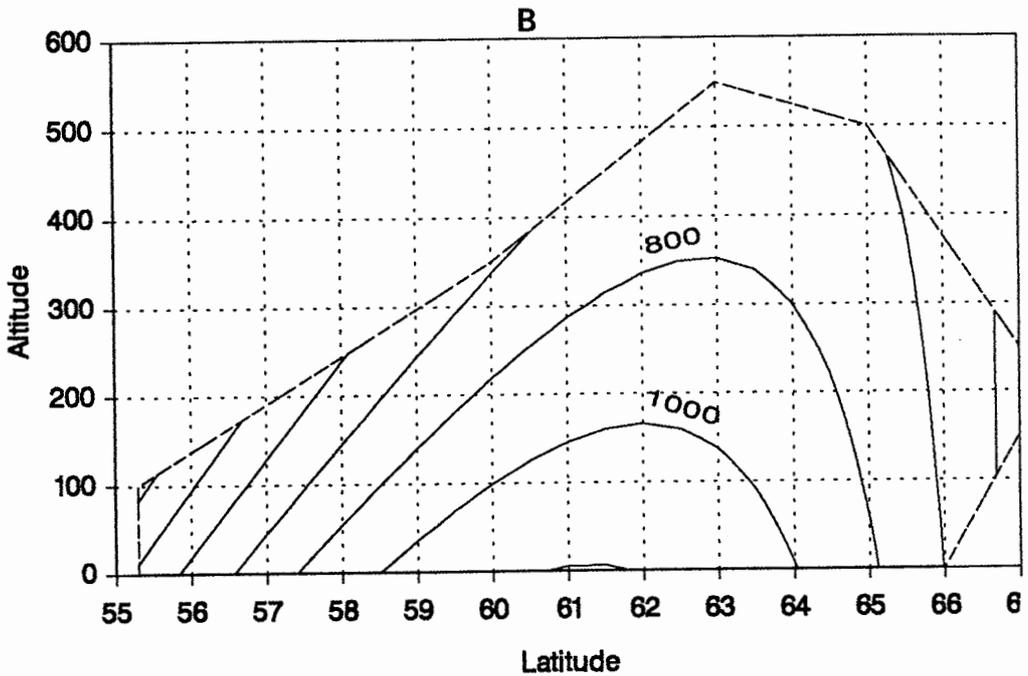
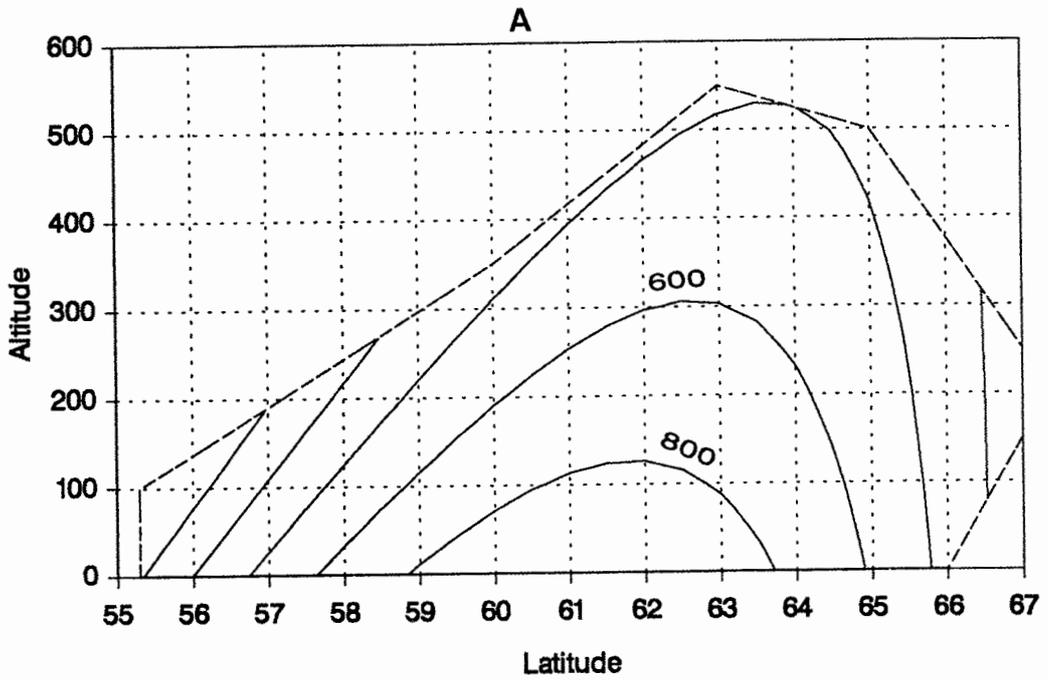


Fig. 7. Model predicting locally the number of straight stems (class 1+2) per hectare (*STR*) at 2.0 m (A) and 1.7 spacings.

$$STR = 676.9 + 246.1 \cdot sp + 64.18 (lat-61) - 27.41 (lat-61)^2 - 1.425 (alt-200) + 0.2481 (lat-61) \cdot (alt-200)$$

$$R^2 = 0.43 \quad Sy \cdot x = 367$$

Discussion

Bends and spike knots in Scots pine stems can have many causes. Although directly inherited abnormalities may be involved, i. e. fasciations, forking or double apical buds (Eklundh-Ehrenberg, 1963), spike knots are generally the effect of a lost terminal bud. The loss could be caused by severe weather conditions, by mechanical damage, by browsing or by attacks of insects or fungi. The probability of developing spike knots is greatest among trees with a prolonged or displaced growth period.

Bends occur when the apical shoot and the cambium compensate for a vertical deviation in the centre of gravity. Although bends are often associated with spike knots, i. e. with a change of leading shoot, they can also have other causes, e. g. the rupturing of roots by snow pressure or strong winds, competition for light, frost heaving on silt soils.

This study is based on assessments of nine trials containing 27 to 29-year-old Scots pine trees of various provenances in Sweden north of latitude 61°N. The plantations were carefully established and have been properly managed. However, it is difficult to decide whether the frequencies of straight stems and trees without spike knots are representative of the Scots pine cultures of the same age within the area, inasmuch as no area-wide survey has been made. The observed frequencies are probably underestimates, because most trials have been fenced and are therefore protected from browsing elk (*Alces alces*).

The mean percentage of trees without spike knots was 47 per cent (Table 3). Trials situated in a severe climate tended to have a frequency below average. Because of low survival on harsh sites, the number of stems per hectare without spike knots (Table 6) was even lower in relative terms. The same tendencies, although less pronounced, were observed for frequency and number of straight stems. On average, 30 per cent of the stems were straight (Table 3, cf. Table 7).

There was significant between-provenance variation within each trial for stem straightness (Fig. 3), and in the majority of trials this was also true for spike knot frequency (Fig. 2).

In general, provenances transferred southward had the greatest number of trees without spike knots (Fig. 4) and with straight stems (Fig. 5) per hectare. On average, for each degree of southward transfer the mean number of trees without spike knots and with straight stems increased by 100 per hectare. However, there was a deviation from this pattern for number of straight stems in trial 15. This trial was characterized by extremely high survival and low

height growth, which has been attributed to the influence of the Atlantic Ocean (Eriksson et al., 1980). A large proportion of the trees was less than 5 m tall, making an assessment of straightness impossible.

Provenances from northern Norway (cf. Eriksson et al., 1980; Prescher, 1986) also deviated from the general pattern. When planted in northern Sweden, they had a low frequency of straight stems, as expected, but the frequency of trees without spike knots was somewhat above average.

The effects of spacing on spike knot frequency and stem straightness are presented in Tables 6 and 7. In general, the percentages of trees without spike knots and with straight stems were somewhat higher at spacing 1.25 m. This is in agreement with earlier studies (cf. Prescher & Ståhl, 1986; Gullberg & Vegerfors, 1987). Consequently, the numbers of straight stems and stems without spike knots were also considerably higher in these blocks.

In Fig. 4 and 5 spacing and transfer effects are compared. In general, a decrease in spacing from 2.0 m to 1.25 m corresponds to a southward transfer of 4.7° and 2.6° as regards the effects on the number of stems without spike knots and the number of straight stems per hectare, respectively. The effect of spacing varied considerably between trails. However, the effect of a decrease in spacing is different from that of a southern transfer. A decrease in spacing will mainly lead to an increase in the total number of stems, while having no effect on the frequency of high-quality stems. At the first thinning, however, the poor-quality stems can be removed, resulting in an increase in the frequency of high-quality stems. This is referred to as "the thinning effect" by Prescher & Ståhl (1986). Before thinning, neither the frequency of straight stems nor the frequency of stems without spike knots differ much between spacings. The effect of a southward provenance transfer is to increase the frequency of high-quality stems. It should be noted that this improvement is a result of the choice of provenance, and does not require future silvicultural treatments. Because the same goal can be achieved by different methods, the forest manager has the freedom to choose according to his particular needs.

When examining the results of the correlation analyses, it should be borne in mind that low values of spike knot number and stem straightness are desirable. The number of spike knots and the degree of stem straightness are strongly positively correlated both at the provenance (Table 4) and at the single tree levels (Table 5). At the provenance level, spike

knot number and stem straightness tended to be positively correlated with growth characters (Table 4), i. e. provenances with tall trees generally have more severe bends than do those with short ones. Note, however, that at the single-tree level the correlations were low (Table 5): height tended to be negatively correlated with numbers of spike knots and bends. Thus, tall trees had few spike knots or few bends. There was no obvious pattern in correlations between the two quality traits and either diameter or stem volume. Nevertheless, at the sites where the relationship between tree height and stem straightness was weak (sites 14, 18 and 21), thin trees had less severe bends than thick trees. Trees can compensate for bends by an increase in diameter. This could explain why the thickest trees had the most severe bends in trials where correlations between height and straightness were weak.

The question of cause and effect arises when the correlation between height or diameter and spike knot frequency is examined. Our opinion is that trees ill-adapted to the climatic conditions are more likely to lose leading shoots or their leading buds than trees which are better adapted. This results in spike knots and reduced height. The number of spike knots due to poor adaptation is generally higher in southern than in northern provenances in this material.

The main trends revealed in this study are similar to those found in southern Sweden (Ståhl & Prescher, 1986). Southward transfer and a decrease in spacing increase the frequency of trees without spike knots and trees without bends. There are differences, however, between regions in the country: On an average, there were approximately ten per cent fewer trees without spike knots and trees with straight stems in the northern than in the southern trials. This is probably an effect of the more severe northern climate. On the other hand, the numbers of trees without spike knots and trees with straight stems per hectare are of the same magnitude both in the north and in the south. Although mortality has been much higher in the northern material (cf. Eiche, 1966), the average number of surviving stems per hectare is higher in the north. The reason for this difference is that the mean height is lower in the northern trials, and consequently, these trials have only been thinned once—if at all. If the comparison had involved trees of the same height instead of the same age, the difference in the number of high-quality stems per hectare between southern and northern sites would have been still more pronounced.

Differences between the effects of human selection

and natural selection on the frequencies of spike knots and bends may be discussed. At thinning there is an opportunity of reducing the number of poor-quality stems. In the provenance series studied, spike knots and severe bends were regarded as strong criteria for removal. If quality is not considered, thinning will not automatically reduce the frequency of trees with spike knots or bends, even though such a reduction is likely to occur, according to the correlation analysis (Tables 4 and 5). In northern Sweden the severe climate is the major factor influencing natural selection. Severe weather conditions can also induce the formation of spike knots and bends. However, there is no evidence that within a provenance, trees with spike knots and bends are competitively less fit than straight trees that lack spike knots. On the other hand, southern provenances of low hardiness are more affected by spike knots and bends than are the more hardy northern provenances.

The generalized models describing countrywide geographical variation in Sweden (Fig. 6 and 7) predict that the number of trees without spike knot and straight stems per hectare should be highest in central Sweden. The most favourable region should lie between latitudes 58°N and 65°N and below 250 m above sea level. In Sweden this corresponds with the region within which values of basic density and tracheid length are highest (Ståhl, 1986). Consequently, the potential for growing high-quality trees is greatest within this region (cf. Ståhl et al., 1986). At higher latitudes and altitudes, the trees are more affected by severe weather conditions.

The low numbers per hectare of straight stems and stems without spike knots in southern Sweden have several causes. The high site quality may result in a prolonged growth period. Consequently, there is a greater risk of unfavourable weather conditions. The greater maritime influence in southern Sweden is also associated with a higher risk of weather damage. The effect of heavy thinning has already been discussed.

It could be argued that the number of trials studied is too small to permit the models to be used for forecasting. Furthermore, there are probably large local deviations from the general trends in the model. The models explain 56 per cent of the variation for stems with spike knots and 43 per cent for straight stems. Deviations due to local environmental conditions may also be substantial. Nevertheless, in our opinion, the models can provide a good overall view of the variation in numbers of straight stems and trees without spike knots in different parts of Sweden.

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