Branch Traits as Selection Criteria in Scots Pine Breeding in Latvia
Zarojuma pazīmes kā atlases kritērijs parastās priedes selekcijā Latvijā

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Abstract. Branch traits are a major factor affecting the grade and value of sawn goods and therefore must be considered in tree breeding. In this study, the relationship among branch and growth traits was analyzed using data from 10 open pollinated progeny trials measured at the age of 14-33 years. Narrow-sense heritability estimates for traits characterizing branch thickness (on average 0.14) and height up to first living branch (0.20) were at the same level as the heritability estimates for tree diameter (0.14), but lower than for tree height (0.45). The coefficients of additive genetic variation for branch thickness traits (11.4% on average) and height up to the first living branch (16.2%) were slightly higher than for growth traits (8.4%) indicating a high potential for the improvement of branch properties through breeding. Selection for height (intensity 10%) would result in a smaller increase of most of the traits characterizing branch thickness than selection by diameter (on average 7% vs 9.1%). Besides, it would improve the branch diameter/stem diameter ratio and the proportional length of green crown (-7.5% and -2.4%, respectively). Selection for height yields in a higher indirect gain in stem volume than does selection for diameter (24.1% vs 5%), and provides a higher gain in stem diameter than would be achieved by direct selection for these trait. Inclusion of tree height and diameter of the thickest branch in a selection index is recommended to secure simultaneous improvement in both growth and quality.
Key words: branch traits, genetic gain, selection index.

Introduction

The good quality of Latvian Scots pine (straight stems, thin branches) has been known for several centuries (Gailis, 1964), and a special natural variety *Pinus sylvestris* var. *rigensis* (Molotkov, Patlaj, 1991) was classified on the basis of these distinct phenotypic characteristics. Attention has been paid to quality traits also in pine breeding, which started in Latvia in the early 1960s. Plus tree selection was carried out by applying an index, in which (in addition to growth) 25% of the tree value was based on natural pruning (the proportional length of the branch-free part), and 25% – on crown quality (Gailis, 1968). These plus tree selections were utilized to establish the first round seed orchards. Surprisingly, almost no difference in branch thickness has been found between progenies of seed orchard seedlots and ordinary stand seedlots at the age of 21 year (Baumanis et al., 2002). Whether this is due to the imprecise evaluation method (visual scoring using 3 grades only) or due to the fact that branch traits are under low genetic control, remains to be resolved.

Progeny trials established to determine breeding values of the Scots pine plus trees are now approaching ⅓ of commercial rotation. Hence, a number of branch characteristics, like height to first living branch, may now be evaluated and more reliable conclusions may be drawn about the quality of the trees at the end of rotation. Since the second cycle of pine breeding is starting in Latvia, it is important to gather information on branch traits. This is needed to create selection criteria for a simultaneous improvement of growth and quality and to predict economic revenues from tree breeding process.

Effects of silvicultural treatments on branch traits of Scots pine, such as initial spacing and the intensity of precommercial thinnings, have been extensively studied in Finland and Sweden. It has been concluded that an increase in the initial stand density of up to 2000-2500 trees ha^{-1} has a marked influence on decrease of branch thickness whereas further increase in the planting density has only marginal impact on branch traits (Jokinen, Kellomäki, 1982; Turkia, Kellomäki, 1987; Oker-Blom et al., 1988). Similar conclusions have been drawn from thinning experiments: branch thickness is reduced when the thinning is delayed (at mean height of 7-8 m instead of 1.2-1.5 m) and when fewer stems are removed in

Table 1

Description of Latvian Scots pine progeny tests used in the study

Trial	Age	Group	Site type	Spacing	Number of families	trees per plot	replica-tions	Survival
1217	14		*Myrtillosa*	1.5×1	36	1	13.4	76
1218	14		*Myrtillosa*	1.5×1	36	1	18.5	55
1111	17	1	*Hylocomiosa*	2×2	37	1	13.7	51
1204A	17		*Hylocomiosa*	1.5×1	37	1	16.5	72
1204B	17		*Cladinoso callunosa*	1.5×1	37	1	17.3	63
30	27		*Vacciniosa*	2×1	80	10	8	44
31	27		*Hylocomiosa*	2×1	80	10	6	45
32	27	2	*Vacciniosa*	2×1	80	8	8	48
28	33		*Myrtillosa*	2×1	283	15	3	34
41	28		*Vacciniosa*	2×1	106	8	6	55

Explanation.

Trial – trial number in Swedish (first 5) or Latvian long-time forest experiment database.

Age – absolute age in time of measurement.

Group – defined for summarizing result tables: in group 1 younger trials with single tree plots, in group 2 older trials with multiple tree plots.

Site type – characterized according to dominant ground vegetation according to Bušs (1976).

Number of trees per plot and replications – harmonic means of number of trees used in analysis (dominant trees in time of measurement).

Survival – for the families included in analysis, %.

No thinning has been done in experimental plots prior to measurement.

the thinning, particularly comparing densities after thinning from about 600 to 3000 trees ha^{-1} (Fahlvik, 2005; Ulvcrona et al., 2007). Even if heavily suppressed branches do not grow much after the first thinning, they remain alive for a long time, which considerably reduces natural pruning rate (Mäkinen, 1999a; Valinger, 1993). Most of the reduction of branch diameter occurs on the first 4-6 m from the stem base (Fahlvik, 2005; Moberg, 1999; Ulvcrona et al., 2007; Uusvaara, 1985). Besides, improving quality through silvicultural methods can only take place at the expense of stem growth (Mäkinen, 1999a, b; Oker-Blom et al., 1988). Considering that the largest share of the monetary value of logs (85% in Finland – Uusvaara, 1985) is determined by volume, seeking quality improvement at the expense of growth is not reasonable. Furthermore, delayed precommercial thinning will lead to financial losses at the time of the first commercial thinning (Fahlvik, 2005) and a longer period for the stand to meet the target average diameter required for final felling (Mäkinen et al., 2005). Therefore, the importance of tree breeding as a method for simultaneous improvement of both branch properties and volume growth needs to be recognized.

Considering the above-mentioned open questions, the aim of this study is to

1) evaluate the genetic determination of branch traits and the possibility to influence them through tree breeding;
2) estimate correlations among branch and growth traits;
3) find selection criteria suitable for simultaneous improvement of growth and branch quality.

Materials and Methods

The study material consisted of 10 open-pollinated Scots pine progeny trials (Table 1) in Latvia (latitude 56°-57°) and in a region in Sweden with similar climatic conditions to Latvia (latitude 56°-60°).

In the trials planted in Sweden, every tree was assessed for height, diameter at breast height (1.3 m), and branch thickness. Branch thickness was evaluated using a 9-grade scale (1 – very thin branches, 9 – very thick branches). The scoring was relative to other trees in the experiment with a similar diameter. In 3 trials (1218, 1204A, 1204B), the thickest branch up to 2 meters height was measured, and in 2 trials (1218, 1204B) the number of branches in the whorl closest to the 1.3 m height was counted. In the Latvian trials, total height, height up to the first living branch, diameter at breast height (1.3 m), and diameter of all branches in the whorl closest to 1.3 m were measured.

Table 2

List of abbreviations used for growth and branch parameters

h	height, m
hgb	height up to first living branch, m
d	diameter at breast height, cm
hd	slenderness ($h·d^{-1}$)
bd	diameter of thickest branch up to 2 m height, mm
bd1, bd2, bd3	diameter of 1st, 2nd, and 3rd thickest branch in the whorl closest to breast height, mm
bn	number of branches in the whorl closest to breast height
gc	length of living crovn, %, ($(h-hgb)·h^{-1}$)·100
bdsum	sum of diameters for branches closest to breast height, mm
bdav	average branch diameter, mm, ($bdsum·bn^{-1}$)
bdtop	average diameter of 3 thickest branches, mm, ($bd1+bd2+bd3$)·bn^{-1}
bdpercx	diameter of thickest branch vs stem diameter, %, ($bd1·d^{-1}$)·10
bdpercm	average branch diameter vs stem diameter, %, ($bdav·d^{-1}$)·10
bg	branchiness in grades
vol	stem volume, m^3

Note. See text for details.

Table 3

Values of genetic parameters, mean and standard deviation in 27-33-year-old Scots pine progeny trials

Variables	Parameters								
	h^2_i	se_i	h^2_{fam}	se_{fam}	CV_a	CV_{pi}	CV_{pfam}	mean	STD
h	0.45	0.05	0.49	0.04	7.8	11.8	5.6	11.9	1.5
hgb	0.20	0.07	0.27	0.05	7.8	16.2	7.5	6.6	1.1
d	0.14	0.04	0.27	0.08	8.9	25.0	8.9	12.3	3.0
hd	0.08	0.01	0.18	0.05	5.6	20.2	7.0	1.0	0.2
bd1	0.17	0.02	0.31	0.04	12.1	30.7	11.2	12.3	3.9
bd2	0.17	0.02	0.29	0.05	12.5	31.8	12.0	10.8	3.5
bd3	0.12	0.03	0.23	0.06	11.0	34.3	12.6	9.4	3.3
bdav	0.15	0.03	0.28	0.05	11.5	30.8	11.4	8.6	2.8
bdtop	0.17	0.02	0.30	0.05	12.1	30.7	11.7	10.9	3.4
bn	0.07	0.04	0.20	0.06	6.7	23.5	7.5	6.1	1.5
gc	0.07	0.01	0.14	0.02	4.8	18.1	6.7	44.1	8.2
bdsum	0.12	0.01	0.23	0.04	12.5	37.5	13.8	54.8	19.3
bdpercx	0.14	0.04	0.25	0.05	10.4	27.4	10.1	11.4	2.9
bdpercm	0.09	0.05	0.18	0.07	8.9	28.1	10.1	7.3	2.0

CV_{pi} – coefficient of phenotypic variation among individual trees.
Presented values are means from 5 trials, weighted by inverse se_i (for h^2_i) and se_{fam} (for h^2_{fam}, CV_a, CV_{pi}, and CV_{pfam}), and medians from all results from particular experiments for mean and STD.

Branch diameter was measured 1 cm from stem, parallel to stem axis. If the branch was lost, but the scar of the branch was easily distinguished, diameter of the scar was measured in the direction parallel to stem axis.

Every tree's position in the stand was recorded. The trees that were clearly suppressed (Kraft class 3 and 4), comprising on average 7% of all the trees in the 14-17- year-old trials and 21% in the older trials, were not included in the analyses. Furthermore, those plots where deaths of trees from root rot have been reported (in 27 years old and older trials), were also not included in the analyses.

Variance components were computed separately for each trial using SAS Proc Mixed and the general linear model:

$$y_{ir} = \mu + F_i + B_r + FB_{ir} + E_{irk}, \qquad (1)$$

where

y_{ir} – trait y measured;

μ – overall mean;

F_i – the effect of family;

B_r – the effect of block;

FB_{ir} – interaction among block and family (plot effect);

E_{irk} – the error term.

Open pollinated families were assumed to consist mostly of half-sibs, consequently $4\sigma^2_F$ was considered to be an estimate of the additive genetic variance (σ^2_A).

Narrow-sense heritability (h^2_i) and its standard error (se_i), half-sib family mean heritability (h^2_{fam}) and its standard error (se_{fam}) as well as coefficients of additive variation (cv_a) were calculated according to methods described by Falconer and Mackay (1996).

A coefficient of phenotypic variation among family means (cv_{pfam}) in percentage was estimated as:

$$cv_{pfam} = \frac{100 \cdot \sqrt{\sigma^2_F + \dfrac{\sigma^2_{FB}}{b} + \dfrac{\sigma^2_E}{bn}}}{\mu}, \qquad (2)$$

where

σ^2_F – family variance component;

σ^2_{FB} – family-block (replication) variance component;

σ^2_E – error variance component;

b – harmonic mean of replications per family;

n – harmonic means of trees per plot.

Additive genetic correlations (r_a) between two traits (x and y) measured on the same individuals from family covariance (cov_{xy}) and family variance components ($\sigma^2_{Fx}, \sigma^2_{Fy}$) were estimated as:

$$r_a = \frac{cov_{xy}}{\sqrt{\sigma^2_{Fx} \cdot \sigma^2_{Fy}}}. \qquad (3)$$

Approximate standard errors for genetic correlations, se_{r_a}, were estimated as:

$$se_{r_a} = \frac{1 - r_a^2}{\sqrt{2}} \cdot \sqrt{\frac{se^2_{h^2_{ix}} \cdot se^2_{h^2_{iy}}}{h^2_{ix} \cdot h^2_{iy}}}. \qquad (4)$$

Genetic gain from backward selection ($\Delta g\%$) was estimated as:

$$\Delta g\% = i \cdot h^2_{fam} \cdot cv_{pfam} \cdot 2. \qquad (5)$$

Correlated gain ($\Delta cg\%$) in trait y when selecting for trait x was estimated as:

$$\Delta cg\% = i \cdot h_{famy} \cdot h_{famx} \cdot r_{axy} \cdot cv_{pfamy} \cdot 2. \qquad (6)$$

Coefficient 2 has been used in formulas 5 and 6, since estimates are based on half-sib families.

Abbreviations used for the variables in the text and the tables are summarized in Table 2.

Results

Genetic and phenotypic parameters, characterizing analyzed variables, are summarized in Table 3 for group 2 trials and described further in text for group 1 trials.

Highest estimate for narrow-sense heritability in both groups of trials was for tree height (0.45). Heritability of stem diameter was more than 2 times lower, and slightly higher in the younger trials (group 1) than in the older ones (group 2) – 0.20 and 0.14 respectively.

Height up to the first living branch in group 2 trials had a slightly higher heritability than diameter (0.20), whereas the relative length of the living crown (in percents of total tree height) had a low heritability (0.07). The single-site estimates of heritability for number of branches per whorl showed much variation among group 2 trials: estimates close to zero (0.02) in two of the trials, and 0.14 in two of the trials. The corresponding estimates in the group 1 trials were slightly higher (0.18, on average).

In the group 1 trials, narrow-sense heritability of diameter of the thickest branch (0.15) was slightly

Table 4

Genetic and phenotypic correlations among traits in 27-33-year-old Scots pine progeny trials

Variable	h	hgb	d	hd	bd1	bd2	bd3	bdav	bdtop	bn	gc	bdsum	bdpercx	bdpercm
h		0.94 (0.02)	0.90 (0.03)	0.11 (0.32)	0.53 (0.27)	0.41 (0.31)	0.33 (0.42)	0.53 (0.28)	0.48 (0.29)	0.14 (0.45)	-0.39 (0.44)	0.47 (0.32)	-0.63 (0.05)	-0.67 (0.10)
hgb	0.57		0.76 (0.07)	0.36 (0.46)	0.37 (0.32)	0.04 (0.23)	-0.26 (0.17)	-0.12 (0.26)	0.13 (0.34)	0.01 (0.35)	-0.74 (0.34)	-0.37 (0.16)	-0.72 (0.20)	0.42 (0.60)
d	0.65	-0.01		-0.25 (0.65)	0.49 (0.32)	0.85 (0.22)	0.79 (0.05)	0.94 (0.15)	0.90 (0.17)	-0.16 (0.02)	0.20 (0.16)	0.30 (0.35)	0.17 (0.43)	-0.37 (0.33)
hd	-0.28	0.29	-0.87		-0.24 (0.39)	N	0.11 (0.73)	-0.30 (0.43)	-0.51 (0.29)	N	-0.87 (0.13)	-0.80 (0.28)	0.20 (0.44)	N
bd1	0.29	-0.04	0.55	-0.52		0.98 (0.01)	0.88 (0.01)	0.97 (0.02)	N	-0.35 (0.24)	0.53 (0.06)	0.71 (0.13)	0.94 (0.10)	0.64 (0.31)
bd2	0.27	-0.05	0.52	-0.48	0.87		0.98 (0.01)	0.96 (0.00)	N	-0.24 (0.34)	0.52 (0.23)	0.97 (0.05)	0.89 (0.19)	0.89 (0.17)
bd3	0.26	-0.03	0.48	-0.43	0.78	0.89		0.91 (0.02)	0.98 (0.01)	0.16 (0.00)	0.43 (0.33)	0.95 (0.01)	0.80 (0.20)	0.62 (0.51)
bdav	0.25	-0.05	0.50	-0.46	0.83	0.88	0.86		0.99 (0.01)	-0.27 (0.03)	0.76 (0.25)	N	0.65 (0.25)	0.15 (0.60)
bdtop	0.27	-0.05	0.53	-0.49	0.93	0.97	0.93	0.89		-0.17 (0.22)	0.45 (0.21)	N	0.87 (0.15)	0.87 (0.22)
bn	0.08	0.03	0.08	-0.06	0.14	0.19	0.25	-0.09	0.20		-0.62 (0.26)	0.40 (0.03)	-0.05 (0.24)	-0.05 (0.00)
gc	0.19	-0.68	0.52	-0.45	0.32	0.23	0.20	0.23	0.24	0.00		0.58 (0.31)	-0.50 (0.39)	0.23 (0.17)
bdsum	0.25	-0.03	0.45	-0.40	0.76	0.83	0.87	0.73	0.86	0.57	0.18		0.41 (0.11)	0.89 (0.28)
bdpercx	-0.26	-0.05	-0.39	0.30	0.54	0.46	0.39	0.45	0.52	0.07	-0.22	0.39		N
bdpercm	-0.26	0.00	-0.35	0.30	0.40	0.46	0.49	0.63	0.48	-0.17	-0.22	0.36	0.80	

Explanation.
Above the diagonal – genetic correlations (r$_a$), standard error in brackets;
below the diagonal – phenotypic correlations;
N – data from only 1 experiment – not presented;
means calculated by weighting by inverse of standard errors in respective trial.

smaller than heritability for stem diameter, whereas practically no difference between these two estimates was observed in the group 2 trials (single-site heritability values for diameter of thickest branch in interval 0.14-0.23). Diameter of the first thickest branch and the second thickest branch in the same whorl showed equal heritability, but for the third thickest branch heritability was slightly lower (0.17, 0.17, and 0.14 respectively), though the number of observations does not differ. Moreover, heritability for the average diameter of the 3 thickest branches and the average diameter of all the branches in the whorl did not differ from heritability of the thickest branch. Heritability estimate for the sum of branch diameters and the relationship between branch and stem diameters was slightly lower than heritability for above-listed branch traits.

Branch thickness assessed in grades (evaluated in group 1 trials) had a notably higher heritability value (0.28) than other branch traits; it is even higher as for stem diameter.

Relative differences among half-sib family mean heritabilities follow the same pattern as for narrow sense heritabilities.

Coefficient of additive variation, determining the potential of breeding to improve a particular trait, was slightly higher for diameter than for height. This difference was smaller in older trials (group 2). Coefficient of additive variation was at the same level also for height to first living branch and number of branches. Low CV_A values were typical for traits with low heritability, such as the length of living crown and slenderness. In group 2 trials, branch traits with equal heritability had also similar CV_A values: diameter of the first and the second thickest branch, the average diameter of the 3 thickest branches; slightly lower coefficient of additive variation is for diameter of third thickest branch and average branch diameter. All this group of branch diameter traits has CV_A values around 30% higher than for height and diameter. In group 1 trials, CV_A value for branch diameter (10.4%) was similar to the one estimated for diameter (10%), but around 30% higher than for height (7%). Coefficient of additive variation for branch thickness in grades (18.6%) was twice higher than for height.

Differences between the phenotypic coefficient of variation and additive genetic coefficient of variation in group 2 trials are lowest for height. For all branch traits differences were similar, except for the sum of branch diameters and the diameter of the 3rd thickest branch, where the differences were higher due to high phenotypic variation.

Genetic and phenotypic correlations among traits are summarized in Table 4.

Tree height had almost twice weaker correlation (both genetic and phenotypic) with most of the parameters characterizing branch diameter (bd2,

Table 5

Genetic gain from backward selection with intensity of 10% in group 2 trials

Variable	Δg%	Δcg% when selected by	
		h	d
H	9.6	9.6	6.4
Hgb	7.0	8.9	5.3
D	8.5	10.3	8.5
Hd	4.3	0.8	-1.3
bd1	12.4	8.2	5.6
bd2	12.4	6.6	10.1
bd3	10.2	4.9	8.7
Bdav	11.2	7.8	10.3
Bdtop	12.4	7.6	10.6
Bn	5.2	1.1	-1.0
Gc	3.2	-2.4	0.9
Bdsum	11.1	7.6	3.6
bdpercx	9.0	-7.9	1.6
bdpercm	6.5	-7.1	-2.9
Vol	24.1	24.1	5.0

Note. See text for details.

bd3, bdav, and bdtop), in comparison to diameter at breast height. The number of branches per whorl had moderate negative correlation with height and diameter (r_a=-0.48 and -0.38, respectively) in group 1 trials. No such relationship was found in group 2 trials. The sum of branch diameters per whorl was also more strongly correlated to height than to diameter (r_a=0.47 and r_a=0.30, respectively).

Genetic correlations among branch parameters (bd1, bd2, bd3, bdav, bdtop, bdsum, bdperx, and bdpercm) were high (r_a=0.71-0.99).

Strong genetic correlation in group 1 trials was found between diameter of thickest branch and branch thickness (r_a=0.77). Branch thickness negatively correlated both with height and diameter (r_a=-0.46 and -0.35, respectively).

Moderate negative genetic correlation was found among the number of branches per whorl and the proportional length of the living crown (r_a=-0.62), but there was no correlation between the number of branches per whorl and the height up to the first green branch (r_a=0.01).

Genetic gain estimates are summarized in Table 5.

Genetic gain characterizes response to selection. In group 1 trials, higher genetic gain can be obtained for diameter than for height (10.8% and 9.4%, respectively), in group 2 trials – vice versa (8.5% and 9.6%). Genetic gain for branch variables (bd1, bd2, bd3, bdav, and bdtop) is slightly higher as for the highest of growth variables (10.4% in group 1 trials, and 11.7% in group 2 trials on average). Response to selection is lowest for the number of branches per whorl, proportional to length of living crown and slenderness.

Height of first living branch and average branch diameter-stem diameter relationship in group 2 trials has only slightly lower response to selection than diameter.

Correlated gain values in group 1 trials indicate that as a result of selection by height trees will have also thinner branches (both – diameter of thickest branch and overall) and also smaller number of branches, in comparison to results of selection by diameter. In analysis of group 2 trials can be seen that selection by height resulted in smaller increase of branch variables (except thickest branch) and larger height to first living branch than selection by diameter. However, selection by height results in stronger increase in sum of branch diameters and branch diameter-stem diameter ratio. Besides, in group 2 trials, selection by height resulted in higher genetic gain by diameter (10.3%) and stem volume (24.1%) than selection by diameter itself (8.5% and 5%, respectively).

Discussion
Genetic Parameters

Tree height is less influenced by stand density (Ulvcrona et al., 2007) than diameter, and a fairly large proportion of its phenotypic variation is genetically determined, as it can be concluded from heritability estimates obtained in this study and several other ones (Haapanen et al., 1997; Danusevičius, 2000; Hannrup et al., 1998; Jansson et al., 2003). Diameter growth of trees is more affected by competition as demonstrated by thinning experiments (Mäkinen et al., 2005; Ulvcrona et al., 2007). Tree diameter (indicating tree position in stand) explains 39-70% of variation in the radial growth among trees. The rest of variation is among trees of the same size (Pukkala, Kolström, 1987). It is reflected as higher phenotypic variation and lower heritability for tree diameter than for height. These differences tend to increase with tree age. It could explain differences in results (differences between heritability of height and diameter) obtained in group 1 and group 2 trials. Similar results have been reported from studies of 11-24-year-old Scots pine trials: unweighted mean for height h^2_i=0.48, and for diameter h^2_i=0.22 (Haapanen et al., 1997). Somewhat higher single-site estimates were found by Haapanen and Pöykkö (1993): h^2_i=0.60 for height, and h^2_i=0.21 for diameter; and somewhat lower as medina from numerous experiments in a review by Cornelius (1994): h^2_i=0.25 for height, and h^2_i=0.18 for diameter.

At the same time in Sweden, analyzing a slow growing Scots pine progeny trial where a thinning was done to even out competition at the age of 33 years, Hannrup et al. (1998) found negligible differences between heritability for height and diameter (0.27 and 0.32, respectively). Also in a 12-year-old *Pinus caribaea* stand (Moura, Dvorak, 2001) with practically no competition among trees (survival – 90-97%), heritability of tree height, diameter and stem volume almost did not differ (0.31, 0.29, and 0.34, respectively).

Heritability for diameter of thickest branch, found in this study, was close to the same as reported in Scots pine trials in Finland: h^2_i=0.14, weighted mean in 11-24-year-old trials (Haapanen et al., 1997); and h^2_i=0.21, in an 8-year-old trial (Haapanen, Pöykkö, 1993). Results ranging from 0.09 to 0.15 have been obtained in Poland (Kowalczyk, 2005). Median of heritability from numerous experiments for branching traits is slightly higher: 0.24 (Cornelius, 1994).

Single site heritability estimates of branch diameter varied from 0.06 to 0.23. It could at least partly be explained by variation in microsite conditions (competition and nutrients) and uneven representation of various conditions by all families in some tests. Turkia and Kellomäki (1987) who

analyzed 17-26-year-old stands, found that the variation in branch diameter was mostly (54%) explained by variation in site fertility rather than by stand density (20%). In this study the site type was a poor predictor of site fertility – branch diameter was closer related to nitrogen concentration in needles.

Branch thickness evaluated in grades had higher heritability than the diameter of the thickest branch in Scots pine trials in Finland (0.26 – Haapanen et al., 1997) and for *Pinus radiata* in Australia (0.27 – Wu et al., 2007), which is in accordance with the results from group 1 trials. Reason for this could be that the evaluation in grades is based on an overall impression about branchiness in different tree parts, but thickest branch, measured at first 2 meters (or in one particular whorl), is an indicator for just a certain development phase of a tree. It does not mean, however, that a measured branch thickness could not be a practically useful indicator: as found by Moberg (1999), local maximum of knot diameter for pine is in height around 2 meters.

Heritability of the number of branches per whorl, found in group 1 trials, is in accordance with results from other studies: for Scots pine h^2_i=0.18 (Velling, Tigerstedt, 1984), for Douglas fir h^2_i=0.19 (King et al., 1992), for Longleaf pine h^2_i=0.21 (Snyder, Namkoog, 1978). However, heritability of this trait was twice lower in group 2 (older) trials. This difference could be explained considering the number of branches per whorl in older trials as composite trait that is influenced by other, at least partly genetically determined, traits:

1) branch diameter – branches with bigger diameter can heave longer (both green and dead) life span and do not fall from the tree that fast (Kellomäki, 1983);
2) radial growth of stem – if radial growth is faster, scars of lost branches are overgrown faster (Mäkinen, 1999b);
3) branch diameter-stem diameter ratio – bigger tree with thinner branches will lose them faster and also scars will be overgrown faster.

Basing on empirical evidence (mean number of branches in group 1 trials is 7.2, in group 2 trials – 6.1) and data from other studies (Mäkinen, 1996; Mäkinen, Colin, 1999; Ulvcrona et al., 2007), it can be concluded that the number of branches per whorl at breast height for 27-32-year-old Scots pine trials is primarily an indicator of branch death and occlusion rate. Therefore, if selection for smaller number of branches per whorl is of interest, evaluation should be carried out at relative early development phase of trees.

Height up to fir st living branch has considerably higher heritability than length of green crown in percents from total tree height. It could be partly explained by the fact that length of living crown (in percents) is influenced by 2 factors – speed of growth and natural pruning rate. Crown recession rate is the dominant factor in equations to differ between good and bad quality stands (Morris, Parker, 1992). Both absolute and relative crown height is increasing by decreasing stand density (Petersson, 1997; Valinger et al., 2000; Ulvcrona et al., 2007), but from this study it can be seen that natural pruning rate has also a genetic component.

Slenderness had a low heritability in comparison to results from other studies, where h^2_i=0.26 (Velling, Tigerstedt, 1984; Haapanen, Pöykkö, 1993). The reason could be that only dominant and co-dominant trees have been used in our study.

Coefficients of additive variation for height, found in this study, are in accordance with previously published estimates for Scots pine: in Sweden from 5.5% (Jansson et al., 2003) to 7% (Jansson et al., 1998), and in Finland – 7.7% (Haapanen, Pöykkö, 1993). Values for diameter for Scots pine (12.1%) and Norway spruce (9.3-11.1%) obtained in Sweden (Jansson et al., 1998; Karlsson et al., 2002) are slightly higher than in this study, but the relationship remains the same – CV_A for diameter being somewhat higher than for height.

Branch traits have similar or even higher values of coefficient of additive variation, indicating high potential for improvement of those traits. Results are in accordance with studies in Finland, where CV_A was estimated to be 6.6-10.4% for the number of branches per whorl and 6.3-7.6% for branch thickness (Velling, 1982). Higher values were reported by Haapanen and Pöykkö (1993) for 8 year old Scots pine trial: for diameter of thickest branch – 18.2%, for the branch diameter-stem diameter ratio – 14.9%. This is in accordance with the trend noted also in heritability values and can be attributed to difficulties in evaluation of branch traits at the lowest part of the stem in older trials, where number of branches and branch diameter are influenced by a set of differing processes: branch radial growth, decay, occlusion. The effect of changing competition circumstances over a longer period of stand growth is added up to the error variance component in the model.

Correlation among Parameters

Decision about the main selection criteria could not be made without understanding, how selection for a particular trait would influence values of other traits in the next generation.

Tree height, in comparison to diameter at breast height, is more weakly correlated (both genetic and phenotypic) to most of the traits characterizing branch diameter (bd2, bd3, bdav, and bdtop). This is in accordance with earlier findings (Velling and Tigerstedt, 1984; Haapanen, Pöykkö, 1993; Haapanen et al., 1997) analyzing diameter of thickest branch in the lowest part of stem (up to 2 meters) in

8-24-year-old Scots pine progeny trials. Results of measurements of sample trees from 61 Scots pine stands in Finland at the age of 35-90 years revealed a similar trend: phenotypic correlation among height and diameter of thickest branch up to 2 meters height was 0.07, whereas between diameter and branch diameter r=0.44 (Uusvaara, 1985). Partly this connection could be explained by variation in branch longevity: radial growth rate of stem is positively related to the duration of branch growth, modified by competition status (Mäkinen, 1999b). Eriksson et al. (1987) in their analysis of a 34-year-old progeny trial in northern Sweden found an opposite result: height had stronger correlation with diameter of the thickest branch in stem section of 1-2 meters from the ground than diameter at breast height. It is similar to results in group 2 trials, where diameter of thickest branch had almost equal genetic correlation with height and diameter, even if phenotypic correlation with stem diameter is almost twice as strong.

Branch diameter (both thickest and mean)-stem diameter relationship has stronger negative genetic correlation with tree height than diameter. This means that faster growing families tend to have lower relative branch diameter. This is in accordance with results from provenance studies (Kohlstock, Schneck, 1994) and progeny trials (Haapanen, Pöykkö, 1993). Height could have stronger negative genetic relationship with branch diameter-stem diameter ratio because faster growing trees would tend to have faster shading of lower branches at a certain height, promoting slow-down of branch radial increment. This assumption is supported by results from thinning experiments, demonstrating that the stand height at the time of thinning is clearly (negatively) related to branch diameter sum/stem diameter ratio in the butt log (Ulvcrona et al., 2007).

Slenderness has 3 times stronger negative phenotypic correlation with diameter than with height. The cause of this could be purely statistical: height is much less variable than diameter for dominant and co-dominant trees analyzed in this study (see cv_{pi} values). The relationship is the same as reported by Velling and Tigerstedt (1984) and Eriksson et al. (1987). Genetic correlation between slenderness and growth traits is associated with standard errors larger than estimates themselves, therefore can not be considered.

Number of branches per whorl has a moderate negative correlation with tree height and diameter, associated with standard errors approximately the same as the estimate. Corresponding phenotypic correlations were positive (r=0.35). Positive genetic correlation with height (r_a=0.26-0.35) and with diameter (r_a=0.31-0.61) was found by Haapanen et al. (1997) and Velling and Tigerstedt (1984). In a situation of equal correlations for height and diameter with

number of branches per whorl selection by height is preferred, since fast height growth ensures also lowest number of branches per meter (Jäghagen, 1997), which could be an important aspect of end use, especially with increasing importance of glued materials. Number of branches per whorl has practically no genetic or phenotypic correlation to height or diameter in group 2 trials. It is the same as reported from older Scots pine progeny trial in Sweden (Eriksson et al., 1987). Absence of correlation could be due to fact that number of branches per whorl at breast height actually represents rate of branch death and occlusion at respective stem section, as discussed previously.

Genetic correlation between height and height to first green branch is stronger than phenotypic, demonstrating that families with best height growth have generated longer logs free of living branches. Tree height is more strongly related with height of green branch than diameter. Since a longer crown increases self-pruning rate below crown base (Mäkinen, Colin, 1999), families having larger height and longer section to first green branch are preferable even if the proportion of green crown from total tree height is bigger. Loose knots are the most important defects reducing timber quality (Sermulis, 2007); a very long time is needed before dead branches self-prune and the process is relatively independent of stand density (Mäkinen, 1999b). Therefore it is of high economic importance to have as long branch-free or dry branch stem section as possible at early age in order to increase the probability of having a long branch-free section at the cutting age.

Genetic correlations among branch parameters (bd1, bd2, bd3, bdav, bdtop, bdsum, bdperx, and bdpercm) are high (r_a=0.71-0.99), which is in accordance with results from studies in Sweden, where r_a=0.68-0.98 for bdav-bd-bdsum (Eriksson et al., 1987).

Diameter of thickest branch has strong correlation with other traits, characterizing branch diameter, comparably lower correlation with mean branch diameter-stem diameter relation and favorable (for selection of good quality) correlation with number of branches per whorl (r_a=-0.35). Correlation with height up to first living branch is moderate (r_a=0.37) and associated with standard error the size of the estimate itself. Absence of diameter of thickest branch-branch number per whorl correlation (-0.04) was reported by Eriksson et al. (1987); however, Velling and Tigerstedt (1984) found a strong genetic correlation between those two variables (r_a=0.32).

Analysis of internal branch structure of mature Scots pines demonstrates that diameter of thickest branch and branch diameter sum per whorl is increasing in first 2-3 m from ground. From this level up to height, that equals site index·2^{-1}-1 or up to base

of live crown, if it is lower, changes in diameter of thickest branch are negligible (Björklund, 1997). It is in a line with finding that allocation of growth to branches increased at the time of canopy closure (Vanninen, 2004) and indicates that diameter of thickest branch in the first 2 meters could be a rather good predictor for branch thickness in the lower part of the tree. Strong phenotypic correlation among diameter of thickest branch in the first 2 meters and thickest dry branch in the whole tree (r=0.73), reported by Uusvaara (1985), as well as strong genetic correlation among diameter of thickest branch and branch thickness in grades (r_a=0.77) in this study suggest that diameter of thickest branch in the first 2 meters could be a good indicator also for general branch thickness of tree. In contrast, Agestam et al. (1998) found low correlation between diameters of thickest branch from different whorl below canopy, and Ulvcrona et al. (2007) reported that diameter of a particular branch is rather dependent on live crown development, for example, in the lowermost crown at certain conditions branches might just stay alive a longer time without producing any viable annual rings (Mäkinen, 1999a). These findings suggest that evaluation of branch thickness in grades is more reliable.

Genetic Gain

Genetic gain figures summarize the effect of heritabilities and trait-trait correlations. Selection for height was found to yield a smaller increase in branch traits (except for the thickest branch), larger increase in the height to the first living branch, stem diameter and stem volume than selection for diameter (group 2 trials). When selecting for height, correlated changes in height, height to the first living branch and stem volume would be slightly higher than half of the standard deviation of these traits, and slightly lower for diameter. Correlated changes in branch traits, in contrast, would be much smaller (on average 0.2 standard deviation units). This indicates that selection for height would not seriously decrease quality, as was also reported by Haapanen et al. (1997). However, if the aim is to improve branch traits, additional variables, such as diameter of the thickest branch, should be included in the selection index. Selection for diameter would produce roughly the same correlated response in branch traits as selection for height, but notably lower response in natural pruning (height up to the first living branch) and growth traits (height, stem volume and diameter itself). The results from group 1 trials mostly are in line with these findings, except that the correlated response in diameter achieved by selection for height would not exceed the gain achieved by direct selection for diameter.

Conclusions

1. Narrow-sense heritability values for traits characterizing branch thickness (on average 0.14) and height up to first living branch (0.20) are at the same level as the estimates for stem diameter (0.14), but lower than for tree height (0.45). Heritability of slenderness, the proportional length of green crown, and the number of branches per whorl are low (0.07).
2. Coefficient of additive genetic variation for branch thickness traits (11.4% on average) and height up to first living branch (16.2%) is slightly higher than for growth traits (8.4%) indicating high potential for improvement of branch properties through tree breeding.
3. Tree height, in comparison to stem diameter, is more weakly correlated with most of the traits characterizing branch thickness (r_a=0.46 and 0.71, respectively) and more strongly correlated with the height up to first living branch (r_a=0.94 and 0.76, respectively).
4. Consequently, selection for height, in comparison to selection for diameter, would result in a smaller increase by most of the traits characterizing branch thickness. It would also improve the branch diameter/stem diameter ratio and the proportional length of green crown. Selection for height results in a much higher correlated gain in stem volume than does selection for diameter (24.1% vs 5%). It also provides higher genetic gain in height up to first living branch and stem diameter as direct selection by mentioned traits.
5. If the aim of selection is to decrease branch thickness, it is necessary and sufficient to include diameter of thickest branch in the first 2 meters in the selection index.

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Anotācija

Zarojuma pazīmes nozīmīgi ietekmē zāģbaļķu šķiru un vērtību, tādēļ tās jāņem vērā, veicot meža selekciju. Pētījumā analizētas sakarības starp zarojumu un produktivitāti raksturojošām pazīmēm, izmantojot datus no 10 priedes brīvappputes pēcnācēju pārbaužu stādījumiem 14-33 gadu vecumā. Iedzimstamības koeficienta vērtības zaru resnumu raksturojošām pazīmēm (vidēji 0.14) un pirmā zaļā zara augstumam (0.20) līdzīgas kā koku caurmēram (0.14), bet mazākas nekā koku augstumam (0.45). Aditīvās ģenētiskās mainības variācijas koeficients zaru resnumu raksturojošām pazīmēm (vidēji 11.4%) un pirmā zaļā zara augstumam (16.2%) ir mazliet augstāks nekā produktivitāti raksturojošajām pazīmēm (vidēji 8.4%), kas atspoguļo nozīmīgu selekcijas darba potenciālu zarojuma kvalitātes uzlabošanā. Atlase pēc augstuma (ar 10% intensitāti) saistīta ar mazāku zaru resnumu raksturojošo pazīmju vērtību pieaugumu nekā atlase pēc caurmēra (selekcijas efekts vidēji attiecīgi 7% un 9.1%), turklāt tā nodrošina arī resnākā zara diametra/stumbra caurmēra attiecības un zaļā vainaga garuma/koka garuma attiecības uzlabojumu (attiecīgi -7.5% un -2.4%). Atlase pēc koku augstuma garantē augstāku selekcijas efektu krājai nekā atlase pēc caurmēra (attiecīgi 24.1% un 5%) un nodrošina augstāku selekcijas efektu caurmēram nekā tieša atlase pēc šīs pazīmes. Selekcijas indeksā rekomendēts iekļaut koku augstumu un resnākā zara diametru, lai nodrošinātu iespējas vienlaicīgai produktivitātes un zarojuma kvalitātes uzlabošanai.