VARIABILITY AND GENETIC DETERMINATION OF SCOTS PINE QUANTITATIVE TRAITS AT THE AGE OF 32 YEARS

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Abstract

Survival, growth (height, diameter at breast height, stem volume, yield) and quality (thickest branch up to 2 meters of tree height, branchiness, and stem straightness in grades) of phenotypically selected Scots pine plus-tree progenies from different regions in Latvia at the age of 32 years have been analyzed. The material was planted in 4 tests in different forest types (*Cladinoso-callunosa*, *Vacciniosa*, *Hylocomyosa,* and *Oxalidosa*) in Kalsnava, eastern part of Latvia.

Average number of trees per family varied from 11 to 21 (survival 18-35%). Mean height for Scots pine at the age of 32 years was 14.2-16.3 m, coefficient of variation – 10-17%, diameter at breast height – 13.1-17.7 cm, 24-32%, stem volume 0.1-0.2 m^3, 49-64%, diameter of thickest branch at up to 2 meters of tree height – 1.3-1.7 cm, 23%.

To secure ability for detection of significant (α=0.05) family differences, average number of trees per family at evaluation age should be at least 24. Narrow sense individual tree heritability (h^2) was 0.11 for stem volume, 0.09 for diameter at breast height, and 0.07-0.11 for diameter of thickest branch up to two meters of tree height.

Best families and individuals were selected for further breeding process. Among-family selection resulted in breeding difference of 37% (80 m^3) in yield and 18% in stem volume without causing changes in quality properties. Combined among-family and within-family selection resulted in double increase of stem volume, improvement of stem straightness of 7-11%, but the selection caused also considerable increase of branchiness (11-42%). Additional testing for material is suggested before using it in further breeding process.

Key words: heritability, survival, growth, quality, improvement.

Introduction

Forest tree breeding in Latvia is being carried out for almost 50 years. During this process phenotypically superior trees (so called plus-trees) have been selected in forests and grafted in seed orchards. To reveal true performance of plus-trees and select best of them for further improvement of economically important traits, progeny tests have been established. According to previous evaluations of some of plus-trees, superior clones have been selected and grafted in second-stage seed orchards to produce seed with higher genetic value.

To continue Scots pine breeding process and increase important traits, it is essential to carry out controlled crossings and increase proportion of favorable alleles for particular trait in genotypes of next generation seed orchard clones. Besides, to secure seed supply and not decrease genetic diversity, it is important to select new sets of clones for second-stage seed orchards for the western part of Latvia. To support both mentioned actions with appropriate material, progeny trials must be evaluated.

There are more than 80 ha of trials established between year 1970 and 1980. They have now reached a suitable stage for evaluation and reliable conclusions can be obtained. Besides, natural differentiation, that reduces number of trees per family, takes place in those experiments. If they are not evaluated soon, there is a high risk that the amount of trees left will not be sufficient for detection of genetic differences and ranking of families. That would cause a necessity to look for new plus-trees in forests and considerably delay establishment of third stage seed orchards with ability to produce seeds with superior genetic value.

There is not only practical, but also scientific (theoretical) interest of evaluation of genetic determination and variability of traits at the age of more than 30 years, since few reports are published about it. Besides, no information about such results from open-pollinated progeny trials of Scots pine has been gained and analyzed in Latvia so far.

The aim of the study is to estimate the level of variability and genetic determination of Scots pine quantitative traits, its genetic determination and effect from within-family and among-family selection (breeding difference); to produce practical recommendations for establishment of new trials, if their final evaluation is planned at the age of 32 years; to select families most suitable for future breeding process.

Materials and Methods

The material consists of 4 tests of open-pollinated progenies of Scots pine phenotypically selected plus-trees from different regions of Latvia, established in years 1973 and 1974 in Kalsnava, eastern part of Latvia. The families (open-pollinated progenies of one mother-tree) are planted in block-plots containing 15 trees (5 trees in 3 rows) in 4 replications. The initial spacing is 2x1 m. No thinning was performed in the experiment. Some of the families are not in all replications, so the total number of families is 56 in Test 1, 50 in Test 2, 49 in Test 3, and 51 in Test 4.

The soil type differs among tests and, according to classification of Latvian forest types based on dominant ground vegetation, is *Cladinoso-callunosa* in Test 1,

Vacciniosa in Test 2, *Hylocomyosa* in Test 3, and *Oxalidosa* in Test 4. All tests are performed on dry mineral soils with gradually increasing fertility from *Cladinoso-callunosa* to *Oxalidosa* (Bušs, 1976).

The trees were measured in 2005, when they had reached age of 32 years. Height, breast height (1.3 m) diameter, and diameter of thickest branch up to two meters of tree height were measured for every tree. Stem straightness and branchiness were evaluated in grades, where 1 – thin branches, straight stem, and 3 – thick branches and stem with 2 or more bends. The evaluation was made relative to trees in the same test. Occurrence of root-rot was reported.

Analysis of variance was performed on each variable measured. The effect of blocks and families was considered as random and calculated with SAS proc glm. The model used in analysis was following:

$$Y_{ijk} = \mu+F_i+B_j+FB_{ij}+e_{ijk}, \quad (1)$$

where

Y_{ijk} – phenotypic observation (height, breast height diameter or branch diameter) of the individual tree from the i-*th* family in j-*th* replication;

μ – the general mean;

F_i – the effect of the i-*th* family;

B_j – the effect of the j-*th* replication;

FB_{ij} – the interaction effect between the i-*th* family and j-*th* replication;

e_{ijk} – the residual effect of the individual tree from the i-*th* family in j-*th* replication.

The assumptions used in the analysis were that the random effects F_i, B_j, FB_{ij}, e_{ijk} are normally distributed with means zero and variances σ^2_f, σ^2_b, σ^2_{fb}, and σ^2_e, respectively.

Variance components were estimated using the restricted maximum likelihood (REML) method (as default in SAS proc mixed). In this method, variance components are estimated by maximizing a marginal (or restricted) likelihood function, that is, a likelihood function obtained after the model has been transformed to eliminate the fixed effects. This method produces unambiguous estimates of variance components from unbalanced data.

Calculations of genetic components were based in theoretical principles described by Falconer (1981).

Additive genetic variance (Va) was obtained as follows:

$$Va = 4* \sigma^2_f, \quad (2)$$

where

σ^2_f – family variance.

Phenotypic variance (Vp) was calculated as the sum of variance components:

$$Vp = \sigma^2_f+\sigma^2_{fb}+\sigma^2_e, \quad (3)$$

where

σ^2_b – block variance;

σ^2_{fb} – family-block interaction variance;

σ^2_e – residual variance.

Narrow-sense heritability (h^2) based on additive genetic effect was obtained as:

$$h^2 = Va*Vp^{-1} \quad (4)$$

Results and Discussion

A good survival of planted material is essential for successful development of the stand. It indicates that the material planted is appropriate (adapted) for particular conditions (Eriksson, 1998). Significant survival differences have been reported among distant Scots pine provenances (geographical transfer) (Shutyaev et al., 2000) as well as among populations and families (Ruotsalainen et al., 1998). The trend is to increase initial spacing (planting less and less trees) in order to reduce costs. The recommendations started from 7000 trees ha^{-1} in year 1971 (Bušs, 1971), and ended up with 3000 trees ha^{-1} currently. For the formation of a forest stand, that means increasing importance of survival of each planted tree. That's why this characteristics needs to be considered first in tree breeding process too.

The average number of trees per family in Test 1 is 21 (survival 35%), in Test 2 – 16 (27%), in Test 3 and Test 4 – 11 (18%). Distribution of families according to their survival is shown in Figure 1.

Jansons (2005) for the same design trial for Scots pine at the age of 32 years in forest type with rich soil (*Hylocomiosa*) reported survival from 5 to 29 trees and in forest type with poor soil (*Cladinoso-Callunosa*) – from 11 to 41 trees. That is in a good agreement with this study.

With the age and increase of dimensions, competition among trees also is increasing, which is the cause of differentiation and natural mortality. To evaluate survival of families at the age of 32 years, it should be considered that in this age the optimal density for Scots pine is approximately 1000 trees ha^{-1}. That means – 14 trees per family in particular tests. To ensure that, the number is increased roughly by 10% – up to 16 trees per family. In Test 1, survival of 16 or more trees per family is shown for 27 families (80% of all analyzed), in Test 2 – for 27 (57%), in Test 3 – for 10 (22%), and in Test 4 – for 7 families (15%). Among these families, the best one according to volume and quality can be chosen for future breeding process and also grafting in second-stage seed orchards.

The stand productivity (yield) depends not only on survival, but also on the speed of growth (productivity). As productivity measures, height, diameter and stem volume have been chosen. The potential to improve growth is related to variation of the mentioned traits (indicated by coefficient of variation) and genetic determination of this variation (indicated by heritability).
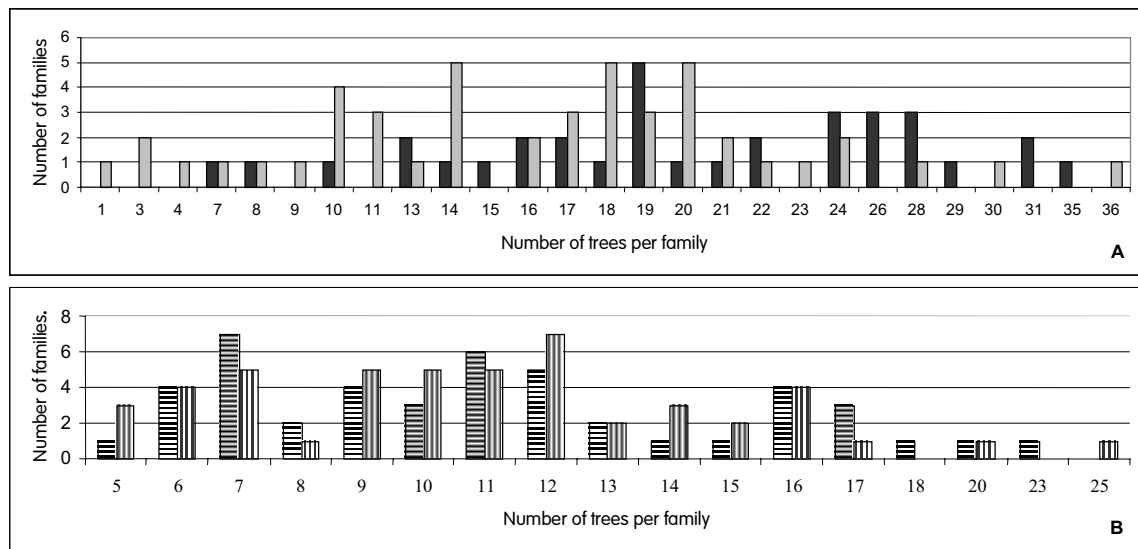
Figure 1. Survival (number of trees per family) of Scots pine at the age of 32 years
A – Test 1 (black columns) and Test 2 (gray columns), B – Test 3 (horizontally dashed columns) and Test 4 (vertically dashed columns).

Variation of traits in all 4 tests is summarized in Table 1, which demonstrates that the variation of diameter is roughly double than of the height, and for stem volume – roughly double that of the diameter.

There is also increasing variation with increasing number of trees observed (in tests with higher survival). Test site with poorer soil (test 1) demonstrated the highest number of trees, lowest mean values and highest coefficients of variation for dimensions of live trees. Poorer conditions lead to a delayed competition factor and consequently lower mortality at the same age. It is in accordance with previous findings in Scots pine experiments in Latvia (Jansons, 2005).

Results demonstrated large variation of productivity traits, which means that selection among individuals to improve mean performance is possible. Not all improvement made by selection can be transferred to next generation. Prerequisite of successful breeding work is heritability of traits – estimation of genetically determined part of total variation. In this case, narrow sense heritability (based only on additive genetic effect) is used, since creation of next generation in industrial scale will take place in open-pollinated seed orchards. With this method only additive genetic effects can be utilized in improvement of genetic properties of seedlings (and future stands).

At first, significance of effects (family, replication, family-replication interaction) in total variance needs to be considered. If family effect is not significant, there is no use from further calculations and among-family selection.

In all 4 tests, to all 3 traits (tree height, diameter at breast height, and stem volume) replication effect had a significant influence. Family-replication interaction had a significant influence in most of the cases (except for stem volume and tree height in test 1 and tree height and breast height diameter in test 3), but family effect was significant only in 3 cases (for tree height in test 4, and breast height diameter and stem volume in test 1). All significances tested were in level $\alpha=0.05$. It is clear that there is an environmental gradient within test sites that influences the average performance and also interacts with families (and is a

Table 1

Variation of quantitative traits for Scots pine at age 32 years

Experiment	Height, m		Diameter at breast height, cm		Stem volume, m^3	
	Mean	CV	Mean	CV	Mean	CV
Test 1	14.2	17	13.1	32	0.1	64
Test 2	15.2	15	15.0	31	0.2	62
Test 3	15.9	12	16.9	26	0.2	52
Test 4	16.3	10	17.7	24	0.2	49

CV – coefficient of variation, %

Table 2

Evidence of block effect - average performance of trees in different replications

Replication	Test 1				Test 2			
	N	H	DBH	VOL	N	H	DBH	VOL
1	124	15.2	15.1	0.15	122	16.6	16.5	0.11
2	164	15.0	14.0	0.12	135	15.8	15.7	0.15
3	179	13.8	12.3	0.10	135	15.3	15.0	0.17
4	180	13.0	11.5	0.08	167	13.9	12.8	0.19

N – *total number of trees;*
H – *average height, m;*
DBH – *average breast height diameter, cm;*
VOL – *average stem volume, m³*

cause of changes of family ranking). The absence of significant family effect could be explained by low survival and consequently insufficient number of observations per family to detect this effect. To test this assumption, all families with survival lower than 16 trees were excluded and new analysis was performed. The analyzed sample from Test 1 contains 27 families and average number of trees per family – 23, for Test 2 – 27 families and 21 tree, Test 3 – 10 families and 18 trees, and Test 4 – 7 families and 18 trees. Analysis is justified also by a previous statement that all families with survival lower than 16 trees will be excluded from future selection due to poor adaptation in particular conditions.

When working with the reduced samples, the coefficient of variation for all analyzed traits has not been changed by more than 2% (except stem volume in Tests 3 and 4, where it was increased by 4%). Mean values of height and volume remained unchanged (except in Test 4 for height – increased by 0.2 m). Breast height diameter increased by 0.4 cm in Test 3 and by 0.7 cm in Test 4. In Test 1, significant family effect was detected to diameter at breast height and tree volume (α=0.05). Replication effect remained significant. In Test 2, replication effect is significant and family effect isn't significant for all traits analyzed. That indicates inaccuracy in selection of area for experiment – there are differences in soil that influence growth of trees. Average performance of trees in different replications in Tests 1 and 2 are presented in Table 2. If only family as a factor was evaluated within each replication in Test 2, its effect appeared to be significant (α=0.05) to all traits in 2 replications.

In Tests 3 and 4, neither family nor block effect was significant. Only significance remains for family-block interaction. It indicates that datasets with particular properties (open pollinated families with survival of only 11 trees per family) are not suitable for detection of among-family differences.

Kowalczyk (2005) for evaluation of genetic effect of Scots pine used trials, where average number of trees in family varied from 68 to 180 at the age of 19-21 years.

For characterization of genetics influence on Scots pine productivity, stem volume and breast height diameter (significant family effect) were chosen. For those traits, narrow sense individual tree heritability (h^2) was 0.11 and 0.09 respectively. The results were lower than those obtained by Costa e Silva et al. (2000) in 15-18-year-old progeny tests of Norway spruce. There h^2 ranged between 0.09 and 0.27 for diameter. Our findings are not in agreement also with the data presented by Hannrup et al. (1998) for Scots pine at the age of 33 years. In this experiment, h^2 for breast height diameter was 0.27, and h^2 for height – 0.32. It can be partly explained by comparably low competition factor among trees – they exposed slower growth (average height of only 10.8 m and diameter at breast height – 10.5 cm) and 1 systematic thinning was done. It can be concluded that for analysis of genetic properties, larger number of trees per family is needed and it can be obtained either by measurements in early age (when crown closure is already formed, but before competition causes mortality) (Svensson et al., 1999) or by planting more trees per family initially.

From Tests 3 and 4, where no significant family differences can be detected due to low survival, individual trees according to their superior performance can be chosen for further testing. Since they are progenies from already selected plus-trees, the probability to find superior productivity is high. Besides, if additional material for breeding population is needed, it is easier to work with those trees than to carry out new plus-tree selection. Since replication effect influenced growth significantly, the best 10 trees according to stem volume were chosen in each replication. That forms a group of 40 trees. To avoid relatedness in future breeding process, only one tree from each family was left. The number of individuals was further reduced to 20. In both steps, trees with lowest volume and, if that's equal, quality were excluded at first. The result of selection is summarized in Table 3.

Among-family selection intensity of 40% (20 from 49) in combination with within-family selection intensity of 10%

(1 from 11) resulted in more than double increase of average stem volume. That indicates large potential of productivity increase by use of chosen trees.

For Tests 1 and 2, where it was possible to detect significant family differences, average results for families were calculated and ranking was made according to stem volume. Families with insufficient survival (less than 16 trees) and planted in less than 3 (for Test 1) or 4 (for Test 2) replications were excluded from top rank. Also if one of stem straightness or branchiness measures were more than 10% below average of the experiment, these families were excluded. Families with highest survival usually tend to have lower stem volume due to increasing competition among trees. To compensate that, the fifth family in ranking according to average stem volume was replaced with the best family in area-based productivity (yield). Among-family selection with intensity of 15% resulted in breeding difference for yield of 37 % (approximately 80 m³*ha⁻¹) and

average stem volume of 18 % in both tests (Table 3). Differences in average height and diameter are in good agreement with the results of the experiment, where average samples from first-stage seed orchards (containing only phenotypically selected clones) and stands were compared (Baumanis et al., 2002). It indicates that the next step of tree breeding (selection of the best plus-trees in orchards according to performance of their progenies) could bring the same high results of the growth improvement of progenies as the first step (selection of plus-trees). In summary, the breeding differences in height growth compared to stands could be as high as 15% (7% in first stage plus 8% in second stage). When using progeny tested clones of Scots pine compared to stand material, a bit more than double increase in genetic gain in height growth has also been found in Finland (Velling et al., 2002). Figures in absolute values (1.6% to 4.2% in Finland compare to 7% and 15% in Latvia) are different, since in Finland only genetic gain (pure

Table 3

Breeding difference among selected and un-selected material of Scots pine at the age of 32 years

Experiment	Selected group and breeding difference	Trait						
		H	DBH	BD	BG	SG	VOL	Y
Test 1	average selected	15.0	14.2	1.3	1.3	1.1	0.13	301
	average all	14.1	13.0	1.3	1.4	1.1	0.11	219
	breeding difference	0.9	1.2	0.0	0.0	0.0	0.02	81
	breeding difference, %	6	9	2	-2	2	18	37
Test 2	average selected	16.2	16.2	1.5	1.5	1.2	0.18	316
	average all	15.3	15.1	1.4	1.4	1.2	0.16	229
	breeding difference	0.9	1.1	0.0	0.1	0.0	0.03	88
	breeding difference, %	6	8	3	5	0	18	38
Test 3	average selected	18.0	25.3	2.1	2.1	1.2	0.42	N
	average all	16.0	16.9	1.6	1.4	1.3	0.20	N
	breeding difference	1.9	8.4	0.4	0.6	-0.1	0.22	N
	breeding difference, %	12	49	27	42	-7	114	N
Test 4	average selected	18.9	26.2	2.0	1.7	1.1	0.47	N
	average all	16.3	17.7	1.7	1.5	1.3	0.21	N
	breeding difference	2.6	8.5	0.3	0.2	-0.2	0.3	N
	breeding difference, %	16	48	18	11	-16	120	N

average selected – average value of particular trait for selected group;
average all - average value of particular trait in all experiment;
breeding difference = average selected - average all;
*breeding difference, % = (breeding difference*average all⁻¹)*100%;*
H – height, m;
DBH – diameter at breast height, cm;
BD – diameter of thickest branch up to 2 meters height, cm;
BG – branchiness in grades, 1-thinn, 3 – thick branches;
SG – stem straightness in grades, 1-streight, 3- double bended;
VOL – stem volume, m³;
*Y – yield, m³*ha⁻¹;*
N – yield in Test 3 and 4 can not be calculated, since individual tree selections have been made

genetic effect) was calculated, but in our case it was the breeding difference.

Latvian pine is well known for its high quality – both straight stems and thin branches. It has been proven also in provenance trials, planting it together with pines from Poland and Germany (Jansons and Baumanis, 2005). That's why the main aim of tree breeding is to increase survival and growth without causing significant decrease in quality for improved material of Scots pine.

For significance tests, diameter of the thickest branch up to 2 meters of tree height (further denoted as branch diameter) was used as indicator, since it was the only quality variable measured (not estimated in grades) and had continuous distribution. In the first analysis of original dataset, a significant block and block-family interaction effect ($\alpha=0.05$) to branch diameter was found, but no family effect was found. Mean branch diameter in Test 1 was 1.3 cm, in Test 2 – 1.4 cm, in Test 3 – 1.6 cm, and in Test 4 – 1.7 cm, coefficient of variation in all cases – 23%. The exclusion of families with survival below 16 trees did not change the situation with significance of different factors. Mean branch diameter decreased in Test 4 (to 1.6 cm) and coefficient of variation in Tests 1 and 4 also decreased (to 22 and 20% respectively). When only family factor influence was estimated in Tests 1 and 2, it was significant ($\alpha=0.05$) in most of the cases (except replication 1 in Test 1 and replications 1 and 4 in Test 2). Narrow sense heritability (h^2) of branch diameter in Test 1 was 0.07 and in Test 2 – 0.11. That indicates rather high potential of selection for quality. Danusevičius (2000) reported heritability of only 0.03 at the age of 12 years and 0.11 at the age of 17 years.

Resulting changes in quality properties after selection of the set of the best families and individuals are summarized in Table 3. Among-family selection (tests 1 and 2) has negligible (5% and less) influence on branch diameter, branchiness in grades and on stem straightness in grades. Combined among-family and within-family selection (tests 3 and 4) resulted in rather high increase in branch thickness and branchiness (11-42%), but led to improvement of average stem straightness (-7 – -16%). When trees were selected, stem straightness was considered more important than branch properties. The soil in Tests 3 and 4 is too rich to recommend for pine growth (forest type *Oxalidosa* is most appropriate for growth of spruce – Bušs, 1976). Together with low survival causes it increases the branchiness

of pine. In comprehensive study of branch properties of Scots pine in Southern and Central Finland, Mäkinen (1999a, b) revealed that the branch growth is prolonged by rapid radial growth of stem. This consequently leads to delayed death of branches – they become thicker and natural pruning is slower. Also wider spacing (e.g. caused by high mortality – as in this case) delayed the reduction in branch growth and increased branch longevity.

That causes difficulties in correct evaluation of branch properties. However, more attention should be paid to branchy trees in future testing and they can not directly be used for propagation in seed orchards.

Conclusions

1. Mean height for Scots pine at the age of 32 years is 14.2-16.3 m, coefficient of variation – 10-17%, diameter at breast height – 13.1-17.7 cm, 24-32%, stem volume – 0.1-0.2 m^3, 49-64%, and diameter of thickest branch up to 2 meters of tree height – 1.3-1.7cm, 23%. It indicates a potential of improvement of mentioned traits along the tree breeding.

2. If average number of trees reaches 24, significant family differences can be detected. This number and average survival must be considered, when the planting of new trial blocks is planned.

3. Narrow sense individual tree heritability (h^2) is 0.11 for stem volume, 0.09 – for diameter at breast height, and 0.07-0.11 for diameter of thickest branch up to two meters of tree height.

4. Best families and individuals have been selected for further breeding process. Among-family selection resulted in breeding difference of 37% (80 m^3) in yield and of 18% in stem volume without causing any changes in quality properties. Combined among-family and within-family selection resulted in double increase in stem volume, improvement in stem straightness – 7-11%, but caused considerable increase in branchiness (11-42%). Therefore additional testing for the material is suggested before using it in further breeding or seed orchard establishment.

Acknowledgements

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