Differential Analysis for Next Breeding Cycle for Norway Spruce in Latvia

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Abstract

Breeding in the most of the Baltic Sea region countries has been used as an important tool to improve target traits of forest trees for more than 60 years. Its basis is an extensive plus-tree selection: in Latvia alone 1700 Norway spruces were identified and their open pollinated progeny tests established. Despite this effort and proven superiority of the selected material, during the last decades share of natural regeneration is increasing at the expense of planting of selected material. Therefore, before entering the next breeding cycle, objective of our study was to optimise the Norway spruce breeding strategy (testing method, duration, family size) under Latvian conditions, and carry out its financial analysis.

Alternative breeding strategies were optimised with the aid of computer simulation and differential analysis comparing planting of selected (improved) material and natural regeneration was applied. Neither duration, nor costs of different alternative strategies were the same, therefore equivalent annual annuity was used as a criterion for comparison.

The simulations showed that the total genetic gain per cycle differs between the breeding strategies: the GEN strategy yielded 9 % more, but the FEN strategy 30 % (testing time 20 years) or 21 % (testing time 25 years) less than the VEG strategy.

For the base scenario in Latvia (the interest rate r = 3 %; the deployment time of the selected material 24 years; the annual planting area is 5500 ha; the genetic gain varies from 25 to 45 %) the equivalent annual annuity from spruce breeding was positive and in range from 2.0 to 12.9 EUR $ha^{-1}y^{-1}$. Even if a 5 % interest rate for investments in tree breeding and seed orchard management were applied, it was more profitable for the forest owner to regenerate areas with genetically improved material than to rely on natural regeneration. Equivalent annual annuity from the VEG strategy was the highest (5.5-12.9 EUR $ha^{-1}y^{-1}$), exceeding that of the other strategies by 34-174 %. Financial gains from any of the strategies increased with expanding area of annual planting as well as with use of silviculture that promotes larger radial increment and in this way shortens rotation length, since the target diameter can be reached faster.

Key words: *Picea abies*, breeding strategy, financial revenue, genetic gain, equivalent annual annuity

Introduction

In Latvia, the first breeding cycle of plus tree selection and progeny testing is completed and a new long-term breeding programme is suggested (Jansons 2008). Concerns have been raised on the profitability of such a long-term investment. Natural regeneration was suggested as a cheap and environmentally-friendly alternative (Nilsson et al. 2002). Considering the long-term benefits of tree breeding, however, the comparison becomes complex and requires an economical investigation. In many countries the advance of breeding resembles the Latvian situation (Jansson et al. 2013) and estimating the profitability of a long-term breeding is an important issue for the developing of national forest strategies (Berlin et al. 2009b). We address this problem by comparing the cost and benefits of regeneration by improved material (including also costs of breeding) and natural regeneration in Latvia. Another goal of our study is to compare several alternatives for breeding differing in their cost, time, and gain-generating capacity. For breeders, this may guide to choose breeding strategy and for financial analysis, to model the profitability of a variable investment in breeding.

To obtain an unbiased financial comparison between planting (using improved planting stock) and natural regeneration, the number of families in breeding population, progenies per family and testing time must be set to achieve a certain breeding efficiency. The genetic progress per unit of time is the most acknowledged indicator of breeding efficiency as it considers the four main factors in breeding: genetic gain and diversity, costs and time (Lindgren and Mullin 1997). To be realistic, the optimisation of breeding should include the breeding method (power to generate the genetic gain), method to accumulate genetic diversity (as the reserve for future breeding), time of testing (longer is more reliable but delays the return) and the costs (the more costs the more gain but large investment) (Danusevicius and Lindgren 2005). The benefit of breeding may be markedly improved by optimising the deployment strategy, when the material is selected from the breeding to the commercial multiplication population: the optimal number of clones in seed orchards, use of seeds from specific crossings or vegetative propagation (Jayawickrama and Carson 2000, Lindgren and Presher 2005). Under the treat of the climatic change, the improved adaptedness of the breeding material provides a long-term value, which is not easy to express in monetary units.

The calculations of the economic benefit from tree breeding were mostly carried out for the fast-growing species (Talbert et al. 1985, Lowe et al. 1999, Todoroki and Carson 2003). In those situations, notable gains have been reported, e.g., the investment in *Eucalyptus globulus* breeding to improve pulp yield provides 10% net benefits (from investment) even when a 5% discount rate is applied (Greaves et al. 1997); the investments in *Pinus ponderosa,* and *Pseudotsuga menziensii* breeding can provide an interest rate of 8% if the material is used for the establishment of short-rotation plantations (Ledig and Porterfield 1982). High revenues from the investments in breeding have also been reported for long-rotation species, e.g., hybrid larch in the northern parts of the USA (Fins and Moore 1984). Economic justification for the use of improved material has been found for *Picea glauca* (rotation period 27-50 years) in a comprehensive analysis, including also silvicultural and soil aspects (Petrinovic et al. 2009). The studies of the breeding aspects of long-rotation species include the analysis of the economic weights of different traits in an optimal selection index for Scots pine in the northern parts of Sweden (Berlin et al. 2009a, Berlin et al. 2009b). The most recent study jointly evaluating the investments in tree breeding and benefits from stands, regenerated with improved material was carried out in Finland (Ahtikoski 2000). This study analysed next generation seed orchards and concluded that the net present values from the investments is going to be positive even with a discount rate of 6% for Scots pine and 4% for Silver birch. Similar analysis for Norway spruce, which is the most widely planted species in the Baltic States as well as in the southern and central parts of Finland and Sweden, is still lacking.

Tree breeding in Latvia has been carried out since the 1950's, focusing mainly on coniferous species: Scots pine and Norway spruce (Zviedre 1988). Importance of Norway spruce has been gradually increasing during the last decades due to the high pulp yield, the lower rate of damages in young plantations and the shorter rotation in comparison to Scots pine. The wood price differences between the two species are minor for some assortments being higher for spruce, some for pine. In Latvia spruce is used in 40 % and 80 % of the total planted areas in state and private forests, respectively (60% in total as an average over the last 5 years). Roughly 27 million plants are being produced annually. The mean annual planting area of spruce is about 5,000 ha. The share of Norway spruce of younger than 40-years-old coniferous forest is 72%.

In Latvia, the decision has been made to use the multiple-population breeding system for widespread tree species, and three breeding populations (altogether 200 trees) have been recruited for Norway spruce (Jansons et al. 2008). In the last decade, the funding of tree breeding was shifted from the direct state funding to project-based. Tree breeding strategy was developed in order to combine different activities that could be funded by separate projects, to ensure an efficient utilization of scientific capacity and financial resources, and to improve the productivity and the quality of the next forest generation (Jansons 2008). Financial evaluation is an essential part of such strategy, especially for Norway spruce, which has one of the highest present and potential use of improved forest reproductive material.

The objective of our study was to optimise the Norway spruce breeding strategies under the Latvian conditions and use it to compare benefit from tree breeding and natural regeneration. Alternatives of breeding strategies was optimised by the aid of computer simulation and compared by differential analysis of the differential costs and revenues of breeding and natural regeneration. It also demonstrates options to proceed with breeding from the traditional plus tree stage into long-term breeding.

Materials and Methods

The breeding population

In Latvia, the present-day breeding population of Norway spruce consists of 1,700 plus trees with open-pollinated progeny trials established 7-11 years ago. 200 out of the 1700 progeny-tested plus trees will be selected to establish three long-term breeding populations. The plans are to mate the breeding population members by single-pair mating (SPM) within each of the three breeding populations separately and proceed with a balanced within-family selection of the two best individuals within each full-sib family as the parents for the next breeding cycle. What remains to be decided and optimised is the breeding strategy to select the two best full-sibs within each of the full-sib families. By the breeding strategy we assume the testing method, the testing size i.e. number of individuals included at different stages of testing process (reflecting the testing precision and the testing costs) as well as the testing time.

Optimization of breeding strategy

Prior to the economic analysis, the breeding strategy was optimised to provide maximum benefit per unit of time at a given fixed budget by the aid of computer simulation. Because the interest rate and the costs were involved in the comparison between breeding and natural regeneration, the costs and timing of breeding became important factors to be optimised. The optimisation was carried out separately for each of the breeding strategies described below and by considering the gain-generating capacity, the time efficiency and the costs of each breeding strategy. The costs were controlled by setting the total budget constraint within one breeding cycle. The final outcome of the optimisation was cycle time and the genetic gain to be used for the financial comparison between planting of improved material and natural regeneration.

The following breeding strategies were compared and optimised by using the inputs for genetic parameters, time and cost components specific to Norway spruce breeding in Latvia (for detailed description of the strategies see Danusevicius and Lindgren 2002b):

(a) phenotype testing (FEN strategy), where the full-sibs (obtained from SPM among the BP members) are field tested and the two best individuals from 300 within each family are selected based on their phenotype;

(b) clonal testing (VEG strategy), where the full-sibs (obtained from SPM among the BP members) are first tested at the nursery stage and after a pre-selection based on the growth rhythm, 40 preselected candidates are cloned to establish the clonal test aimed to select two best individuals within each family based on the performance of their clonal copies.

(c) progeny testing (GEN strategy), where the full-sibs are tested in two stages: first, the pre-selection based on phenotype by exploiting the time until the candidates reach their sexual maturity and second, progeny testing of 25 of the preselected candidates in a new test to select two best full-sibs within each family based on the performance of their open pollinated (OP) progeny.

The target parameter to be maximised when searching for the optimum testing time at a given budget was the genetic gain per year (*Gain/Y*):

$$Gain/Y = G / CT, \qquad (1)$$

where *G* is the estimated additive genetic gain at rotation age, % (cumulative for the two testing stages in VEG and GEN strategies);

CT is the breeding cycle time consisting of the following: the recombination time among the breeding population members, time before testing to produce plants and the testing time.

The genetic gain at rotation age from within family selection following each breeding strategy was predicted according to the following formulas (Lindgren and Werner 1989):

Selection based on phenotype:

$$G = \frac{\sigma_{Am}\, r_{j-m}\, i\sigma_A}{\sqrt{\sigma_A^2 + \sigma_D^2 + \sigma_E^2}} \qquad (2)$$

Selection based on clonal test:

$$G = \frac{\sigma_{Am}\, r_{j-m}\, i\, \sigma_A}{\sqrt{\sigma_A^2 + \sigma_D^2 + \frac{\sigma_E^2}{n}}} \qquad (3)$$

Selection based on half-sib progeny test:

$$G = \frac{\sigma_{Am}\, r_{j-m}\, i 0.5\sigma_A}{\sqrt{0.25\sigma_A^2 + \frac{0.75\sigma_A^2 + \sigma_D^2 + \sigma_E^2}{n}}}\ , \qquad (4)$$

where: *G* is additive genetic gain (%), σ^2_A is additive variance, σ^2_D is dominance variance, σ^2_E is environmental variance, *n* is number of plants per family, σ_{Am} is standard deviation in breeding value of the selected individuals for a target trait at rotation age and is given as percentage of the average breeding value of the unimproved individuals for this trait (one standard deviation is equal to 10%), *i* is selection intensity estimated in the units of standard deviation of the mean of the selected individuals from the family mean by the aid of an approximation by Burrows (1975), r_{j-m} is juvenile-mature (J-M) genetic correlation estimated according to the formula developed by Lambeth (1980) and parameters based on the study of Scots pine by Jansson et al. (2003).

The cycle cost assumed to include the following:

$$C_{CYCLE} = C_{RECOMB} + C_{INIT} + n\ (C_G + m\ C_P), \qquad (5)$$

where: C_{RECOMB} is cost for recombination among the founders, C_{INIT} is cost for initiation of the test, C_G is cost per genotype used for VEG and GEN strategies only and assumed to cover production of the ortets for further cloning and testing or production of female parents and the OP seed collection for testing), C_P is cost per test plant assumed to cover the following:

production of the test plants in the nursery- seedlings (FEN, GEN strategy) or cuttings (VEG), establishment, maintenance and assessments of the selection test, *n* is number of genotypes (ortets for clonal test of female parents for progeny test), and *m* is number of plants (number of ramets per clone in clonal test or number of seedlings per family in progeny test).

For the simulations, the costs were expressed in "plants" (one plant in the field) as the cost units. The testing cost was assumed to be proportional to the test size in "plants" as the cost units. The other costs were expressed as the proportions of the plant cost (Table 1).

The fixed inputs in the optimisation were the genetic parameters, the time of recombination and the time before and after testing. The fixed inputs were set based on practical breeding in Latvia (Table 1).

The variable input to be optimised was the testing time to return maximum annual genetic gain under the given budget. The optimization was carried out at a budget constraint, which was expressed as restrictions on number of families (200) and trees per family (≤ 300 plants), and the number of the pre-selected full-sibs (≤ 40 plants) and the cost per pre-selected full-sib family member (≤ 1,600 plants). These restrictions were based on budget and management constraints as well as on intended selection intensity after the first breeding cycle.

The cost of each breeding alternative was transferred into euros calculating the monetary value of one plant in the field test, based on economy of practical breeding in Latvia obtained from JSC "Latvia's State Forests". These costs of each breeding alternative were used in further economical calculations.

The breeding strategies were optimised by the aid of a deterministic computer simulator Breeding Cycle Analyzer, where values of genetic parameters (additive genetic variance, juvenile-mature correlation, heritability etc.) and values describing breeding population (times to complete parts of the breeding cycle, number of families etc.) are used as input parameters. Calculation method and formulas used are described both in publication by its developers (Danusevicius

Table 1. The parameters and their input values

Parameters	FEN	VEG	GEN	Comment
Narrow-sense heritability (h^2)	0.24			Based on trait index spruce age 32 in Latvian trials
Additive standard deviation at mature age (σ_{Am}), %	10			Westin and Sonesson, 2005
Rotation age, years	60 (or when 30 cm diameter is reached)			Norway spruce rotation age in Latvia
Recombination time, years	6	6	6	Mating among breeding population members
Time before testing, years	2	2	2	Production of test plants in nursery
Testing time for selection (FEN) or pre-selection (VEG, GEN)	20*	2*	14*	Optimized with restriction to be > than 9 years[1]
Time to obtain progenies, years	-	1	8	Time to get cuttings (VEG), seedlings (GEN)
Testing time at stage 2, years	-	12*	12*	Optimized with restriction to be > than 9 years
Time for deployment, years	18	18	18	Time to obtain seed orchard producing the improved seeds
Total breeding and deployment time, years	**46**	**41**	**60**	**Sum of the above**
Cost per plant (Cp), "plants"	1			All other costs are expressed as proportion
Recombination cost, "plants"	30			Ratio of 1
Cost per genotype (Cg), "plants"	-	3	5	Ratio of 1
Number of families	200	200	200	Created after DPM among BP members
Family size	300	100	120	
Family size after pre-selection	-	40	25	Set based on physiological and budget constraints
Number of individuals for BV testing of each pre-selected full-sib	-	40	35	
Genetic gain at rotation age, %	The value at maximum GMG/Y was used in the financial analysis of comparison of net benefit from breeding and natural regeneration			
Genetic gain per unit of time, %	To be maximized when optimizing breeding			

* time components, which were optimized and represent the results of this study.

[1] the restrictions of testing time (≥ 9 years) were based on studies by Danusevicius and Lindgren (2002b), Haapanen (2001), Jansson et al. (2003). The exception is VE at the pre-selection stage, where it represents the nursery testing to exploit the time while the hedges reach their minimum reproductive capacity.

and Lindgren 2002a) and in the tool itself (available on the WEB at http://daglindgren.upsc.se/Breed_Home_Page/Breeding_Cycler/).

Financial comparison between breeding and natural regeneration

The differential analysis of planting of improved material and natural regeneration considered the breeding work, seed orchard establishment and maintenance, and the stand tending costs. The cost structure was obtained from JSC "Latvia's State Forests", which is funding the Norway spruce breeding, owns nearly all the seed orchards in Latvia and manages 82% of the annual spruce planting areas in Latvia (Gadskārta 2014). We also use realistic cost estimates of breeding work drawn from Latvia's breeding programme (Jansons 2008).

The genetic gain in wood yield at the rotation age of the genetically improved stands was expressed as a percentage of the wood yield of unimproved naturally regenerated stands by summing up the following: (a) the genetic gain of 10 % already possessed by the progeny-tested breeding population members at the start of the first breeding cycle; these 10 % were based on the empirical evidence (Jansons et al. 2008), (b) the genetic gain per breeding cycle generated by the within-family selection the following FEN, VEG or GEN breeding strategies, obtained from the computer simulation (formulas 2-4 above), and (c) the genetic gain from the among-family selection, when selecting the clones from the breeding population to the seed orchards assuming to contain an optimum of 20 clones, obtained by estimation (selecting the best 20 families out of 50) using the method described by Viana et al. (2009). This compound genetic gain represents the improvement after the first breeding cycle. Considering the possibility of large investments, the potential to gradually improve the genetic gain after the advanced breeding cycles. variable financing situation (the more input the more gain) and stochastic factors, a range of values of genetic gain was tested. Wood yield of the unimproved stands at rotation (in m^3 ha^{-1}) was obtained from National Forest Inventory (NFI 2014) and, for the improved material, the genetic gain was translated from percentages to the cubic meters per hectare. The genetic gain in stem quality was not considered.

The differential approach was used, i.e., only the positions of the benefits and the costs, which differ between natural regeneration and tree breeding, were considered (Ahtikoski 2000). To carry it out, all planned activities (starting from crossing to obtain test material for breeding cycle), time (year from the beginning of breeding cycle to its accomplishment and further to establishment and growth of seed orchard, planting and management of the stand from its seeds) and their respective costs were listed. For further calculations differential costs of breeding were considered, including the costs of (1) breeding according to particular alternative (FEN, VEG, GEN); (2) seed orchard establishment and maintenance based on scientific recommendations (Baumanis and Birģelis 1993a); (3) plant production, soil preparation, planting, and two extra cleanings. The differential benefits of breeding were additional wood yield and shorter rotation time of the stands established with the improved material.

The traditional, low intensity and the targeted silvicultural systems were used in analysis. The targeted system is aimed to maximize the volume of trees at felling and is characterized by low initial stand density (Zālītis and Jansons 2009). The thinning regimes were chosen the same both for naturally regenerated stand and planted (improved) stand, according to the recommendations (Zālītis and Jansons 2009) The rotation time was decided according to the age or the target diameter of 30 cm, if it is reached earlier (according to the current legislation of Latvia), see example in Table 2.

Table 2. Predicted growth for Norway spruce stand with different silvicultural system

Age, years	N		D, cm				Wood removal, m^3ha^{-1}			
	Trad.	Targ.	Trad.		Targ.		Trad.		Targ.	
			nat.	br.	nat.	br.	nat.	br.	nat.	br.
30	3800	1600	11	12.2	17	18.9	80	116	-	-
50	1100	1100	19	21.1	23	25.5	90	131	220	319
80	650	650	26	28.9	30	33.3	420	525	550	690*

*final cut by target diameter at the age of 70 years; silvicultural system: Trad. means traditional (used in practice), Targ. means targeted; N is the number of trees before the cut; D is average diameter; nat. means regenerated with un-breed material; br. means regenerated with breed material (genetic gain is 25%)

The assortment structure in thinning and final felling was calculated by the algorithm developed by Ozoliņš (2002). The assortment prices: the first grade logs (top diameter exceeds 31.9 cm) – 55.2 EUR m^3, the second grade (19-31.9 cm) – 54.6 EUR m^{-3}, the third grade (14-18.9 cm) – 49.9 - 55.2 EUR m^{-3}, pulpwood (6-13.9 cm) – 26.9 EUR m^{-3}, firewood (3.0-5.9 cm) – 14.1 EUR m^{-3}.

The seed needs for plant production in future were estimated assuming that all spruce forests on fertile soils (site index H_{100} = 30 m or larger) would be clear-felled and replanted with improved spruce. The seed orchard area was selected based on predictions about the seed needs for plant production: taking into account long term observations of seed crops: frequency and seed bulk (Zviedre 1988).

Because of different length of investment period the differential benefit of breeding was calculated as the difference of equivalent annual annuity (EAA) (Klemeperer 1996) of the differential benefits (discounted income) and the differential costs (discounted costs) (both expressed in euros per ha). The interest rate of 3% was used.

The values in Table 1 together with the corresponding cost estimates were used to calculate the differential benefits from the tree breeding alternatives.

Results

Comparison of the breeding strategies

The simulations showed that the total genetic gain per cycle differs between the breeding strategies (at the same cost, optimum testing time and other inputs in Table 1): the GEN strategy yielded 9 % more, but FEN strategy 30 % (testing time 20 years) or 21 % (testing time 25 years) less than the VEG strategy.

The testing time was an important factor to be optimized when maximizing the genetic gain per unit of time for all the breeding strategies. For the FEN strategy, as much as 26 % of the maximum achievable genetic gain can be lost if the testing is 9 years long in comparison with the optimum of 20 years. For the VEG strategy, the testing time for the pre-selection was kept fixed to 2 years and the optimum of 12 years was found for the stage 2 testing (Table 1). For the GEN strategy, finding the optimum was a more complex task to combine the testing time for pre-selecting the full-sibs and the time for testing their open-pollinated progeny. The testing time at the pre-selection turned to be an important factor, where 9 years of testing would generate 89 % of the maximum gain achievable at the age of 14 years. In addition to the high genetic gain, the VEG strategy also had the shortest breeding cycle time of 23 years (Table 1).

Simulations showed that the input in breeding expressed here as the size of the tests, also had a marked effect on the genetic gain. Large tests were needed to maximize the genetic gain from the FEN alternative (Table 1). The VEG alternative also required a high number of trees per family (200), but it is reduced for further calculations considering that the pre-selection period is just 2 years long. The reduction of the number of trees per family from 200 to 100 resulted in 0.8 % change in the total costs of the tree breeding work in this alternative. The number of candidates (trees from each full-sib family, selected for progeny testing) is 1.6 times higher in the VEG alternative, than in the GEN one. Optimal number of ramets per candidate in the VEG alternative is 30, but the number was subjectively increased to 40 considering the test in various environments, even if it results in a 21 % increase in costs of the tree breeding work in this alternative.

The financial evaluation

For the base scenario in Latvia (the interest rate r = 3%; the deployment time of the selected material 24 years; the annual planting area is 5,500 ha; the genetic gain is in the range between 25 and 45 %) the equivalent annual annuity from spruce breeding was positive and in range from 2.0 to 12.9 EUR ha^{-1}y^{-1}, depending on the breeding strategy (Figure 1a).

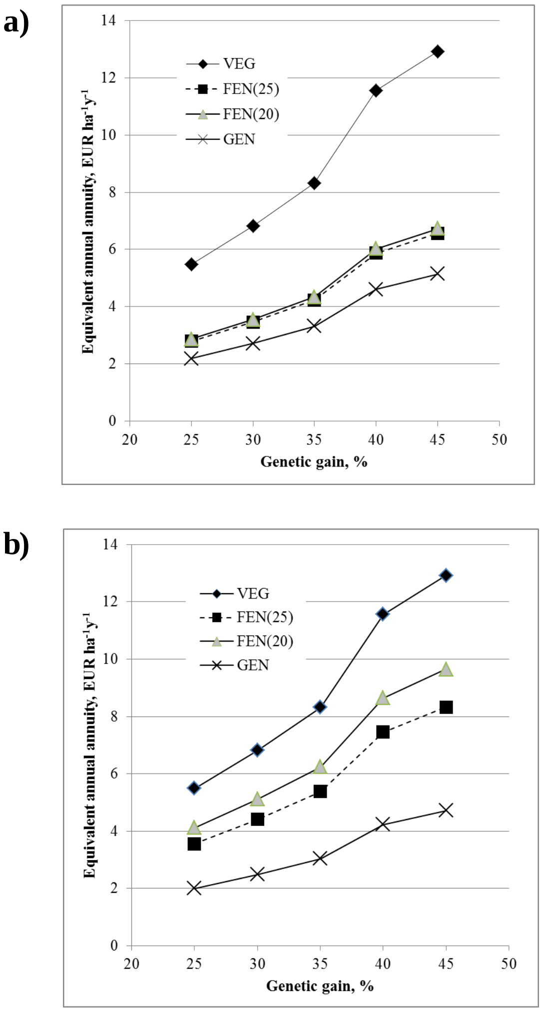

Figure 1. The equivalent annual annuity from alternative Norway spruce breeding strategies in comparison to natural regeneration at their optimal values (a) and at equal values of genetic gain (b).

VEG is clonal testing; FEN (25) and FEN (20) are phenotypic selection with 25 and 20 year testing time and the genetic gain 79% and 70%, respectively, of that in VEG alternative; GEN is progeny testing, genetic gain 109% of that in VEG alternative; FEN (similar 25) and FEN (similar 20) are phenotypic selection with 25 and 20 year testing time, genetic gain the same as in VEG alternative; GEN (similar) progeny testing, genetic gain the same as in VEG alternative. Interest rate r = 3%. The deployment time of the improved material is 24 years; annual planting area is 5,500 ha

In all the cases analysed, the equivalent annual annuity from the VEG strategy (clonal testing) was the highest, ranging from 5.5 to 12.9 EUR ha^{-1}y^{-1} and exceeding the other breeding strategies by 34-174 % (Figure 1ab). The lowest values of the equivalent annual annuity were found for the progeny testing (GEN), the FEN strategy (phenotypic selection) with 25 years of testing time yields slightly higher equivalent annual annuity, followed by the same selection alternative with 20 years of testing time (Figure 1a). The ranking did not change, but differences were more pronounced, when equal values of genetic gain were assumed for all the breeding strategies, without changes in any other parameters (Figure 1b).

Variation in annual planting area markedly affected the equivalent annual annuity from all breeding strategies (Table 3). Planting the improved material of Norway spruce on the annual planting area of 5,500 ha (usual spruce annual planting in Latvia) would ensure from 10 % (with traditional silviculture) to 28 % (with targeted silviculture) higher equivalent annual annuity than planting it on 10 % of this area (Table 3). This relation between the annual planting area and the differential benefit was not linear: the increase of the planting to a theoretical maximum of 7,000 ha (the average annual area of all clear-cuts of spruce stands on mesotrophic soils) raised the equivalent annual annuity only marginally (Table 3). However, the increase of annual planting area to 7,000 ha may raise the total income for the land owner considerably (by 27 %) over the 24 year period, which is the operational period of the seed orchards.

Table 3. The differential benefit from tree breeding in comparison to natural regeneration, EUR ha^{-1}

Silvicultural system	Annual planting area, ha	Tree breeding strategy		
		FEN (gain 32%)	VEG (gain 40%)	GEN (gain 44%)
Traditional	550	1.7	7.0	2.8
	1000	2.1	7.7	3.1
	2500	2.3	8.3	3.3
	5500	2.4	8.5	3.4
	7000	2.4	8.5	3.4
Targeted	550	8.0	13.2	5.2
	1000	8.4	13.9	5.5
	2500	8.6	14.4	5.7
	5500	8.7	14.6	5.8
	7000	8.7	14.7	5.8

Tree breeding alternatives: FEN, GEN, VEG with the level of genetic gain in volume production given in the brackets. The value of genetic gain for VEG alternative is set from the interval of probable gains and corresponding values (at equivalent costs and optimum testing time) for other alternatives calculated (see text for details). The interest rate, r = 3%. The time of use of the seed orchard seed material in plantation, establishment (deployment time) is 24 years

The improved material must be treated with an appropriate silvicultural system to reap the highest economic benefits from the planted forests. If the annual planting area exceeded 1,000 ha, the equivalent annual annuity from the stands with targeted silvicultural system increased from 0.7 to 0.8 times (in the GEN and VEG strategies, respectively) to 3.0 times (FEN strategy) in comparison to the traditional silvicultural system (Table 3). The main reason for this difference was that the targeted silvicultural system promoted rapid radial growth, and it was possible to shorten rotation age (by up to 20 years – from 80 down to 60 years), while final felling was based on target diameter.

An analysis of the VEG strategy (clonal testing) revealed that the internal rate of return (IRR) from the investment in breeding, based on the differential benefit, increases with increasing genetic gain and planting area (Table 4). In case of annual planting area of 550 ha, the traditional silvicultural system and genetic gain below 40 %, IRR was lower than 3 %. Planting in the areas as currently in Latvia, the genetic gain of 25-45 % ensured IRR from 3.4 to 5 % with traditional and from 5 to 5.7 % with targeted silvicultural system. If only half of the area was treated with the targeted silvicultural system, IRR more than 5 % was guaranteed. In this case it does not mean that by using genetically improved material it is possible to earn 5 % per year from investments in forestry. It means that even if a 5 % interest rate for investments is applied, it is more profitable (larger revenues) for the forest owner to regenerate areas with genetically improved material and not to rely on natural regeneration.

Table 4. The internal rate of return for differential analysis in clonal testing (VEG) strategy with different levels of genetic gain

Silvicultural system	Annual planting area, ha	Genetic gain, %				
		25	30	35	40	45
Trad.	550	2.2	2.5	2.7	3.2	3.4
	5500	3.4	3.8	4.1	4.9	5.0
Targ.	550	3.2	3.4	3.6	3.7	3.9
	5500	5.0	5.2	5.4	5.6	5.7

Silvicultural system: Trad. means traditional, Targ. means targeted. The time of use of the seed orchard seed material in plantation establishment (deployment time) is 24 years

Discussion and Conclusions

Our results show that the investment in tree breeding is profitable not only by considering the genetic factors but also by incorporating the financial tools in the comparison. Below, we discuss strong and weak points of our findings in the light of additional considerations, which were too complex to be given a numeric value and incorporated in a simulation or economical comparison.

The testing time

The economic revenue from breeding as well as the comparison among the breeding strategies is strongly influenced by the testing time and testing size. Therefore, it is important to use reasonable values of testing time and testing size to avoid overestimations in the economic gain, especially for the most profitable VEG breeding strategy. Among other factors, the genetic gain from the tree breeding strongly depends on the juvenile-mature (J-M) genetic correlation, which in turn is dependent on the testing time. The heritability and J-M genetic correlation of breeding traits tend to increase with age (Hodge and White 1992, Haapanen 2001, Jansson et al. 2003). Selection at an early age, however, allows realizing genetic gain faster, but its value is reduced due to lower selection accuracy. Such selection leads to similar increase of coancestry in the breeding population as more accurate selection at later stages of tree growth (Wei and Lindgren 2001). The selection age of 11 years has been recommended as optimal for progeny testing of Scots pine in Sweden, based both on the productivity and wood properties (Hannrup and Ekberg 1998, Jansson et al. 2003). It is in agreement with the earlier recommendations for Scots pine in Latvia (Baumanis and Birģelis 1993b). A slightly shorter testing time for clonal tests could be used (Ståhl and Jansson 2002). A selection when trees have reached the height of 3-5 meters has been recommended for all widespread tree species in Scandinavia (Lindgren 1984, Stener and Jansson 2005).

From the financial point of view, the optimal testing time depends on the testing method and interest rate applied to the investments in tree breeding. The optimum testing time is longer when the interest rate is low (2% rather than 8 %) and when the selection is based on phenotype (FEN) instead of the progeny or clonal testing (GEN or VEG) (Haapanen 2001, Jansson et al. 2003). Our results are in agreement with the above-given general conclusion (Table 3), but, in case of FEN strategies also demonstrate the decrease of equivalent annual annuity because of too long testing time (25 years) not compensated by increased accuracy of selection (and genetic gain). Comparably long testing time of 20 years in the FEN strategy has been recommended also in Lithuania (Baliuckas et al. 2004) and in the simulation studies, based on the information from the Swedish Norway spruce breeding program (Danusevicius and Lindgren 2002a). The study of Danusevičius and Lindgren (2004) also showed that intensive flowering simulation to shorten the GEN strategy is beneficial only in case, if flowering can be reached at the age of less than 5 years. It is not realistic for Norway spruce; therefore a longer testing time has been used (Table 1). It is also concluded that the pre-selection of ortets for the clonal testing (the first testing time in the VEG strategy) does not yield an additional gain and should be avoided (Danusevičius and Lindgren 2002b). In our study we retained the pre-selection phase for VEG alternative to allow preliminary screening for selection of adaptive traits, like, e.g. growth rhythm that is under strong genetic control and is closely linked to the occurrence of frost damages and frequency of ramicorns in situations where the genotype does not fit the climatic conditions (Ekberg et al. 1984, Danusevicius and Persson 1998, Hannertz et al. 1999).

The testing size

In the Danusevicius and Lindgren (2002a) simulation based on Swedish spruce breeding strategy, the optimum full-sib family size after the controlled crossing among the breeding population members was 182 candidates in the FEN strategy; 11 candidates to be tested with 47 progenies each in the GEN strategy and 20 candidates to be tested with 15 ramets each in the VEG strategy. In the simulation heritability of the target trait 0.1 has been used, noting, that higher heritability would require lower number of trees (FEN), progenies per candidate (GEN) or ramets per ortet (VEG). In our study, a higher heritability as well as larger test size (larger number of individuals) were used (Table 1). This strategy allows testing the material at several environments and incorporating the plasticity and the genotype-environment interaction in the selection index.

Even within a climatically narrow zone, the environmental variation is such that "neither 2 planting sites, nor 2 years of planting are the same" (Matheson and Cotterill 1990). This can be described by the type B genetic correlation (r_b) between the testing sites, which implies the reduction of genetic gain when the selections based on the results in one site are used on another site. In conifers, the type B genetic correlations are low even between trials within one breeding zone and between the traits with high heritability, for example, r_b = 0.37-0.61 for height, r_b = 0.36-0.58 for diameter of Norway spruce (Karlsson and Högberg 1998); r_b = 0.61, standard deviation 0.39 (Haapanen 1996) and r_b = 0.38-0.97 (Zhelev et al. 2003) for height of Scots pine. These results suggest that the testing must be carried out in several trials within the breeding zone to improve precision of the breeding value. A relatively low number of ramets per ortet (1-10) in several testing sites (4-6) are defined as optimal in several studies (Russell and Loo-Dinkins 1993, Isik et al. 2004, 2005, Stener and Jansson 2005). The risk to loose trials due to browsing or vole damage, forest fire or other random factors must be taken into account by increasing the quantity of necessary ramets (Zhelev et al. 2003).

How realistic are the predicted genetic gain?

As in our study, the superiority of the clonal testing (VEG strategy), have been found in other studies computer simulations with similar scenarios where the genetic gain per unit of time or efficiency of breeding process have been used as indicators (Figure 1, Rosvall et al. 1998, Danusevicius and Lindgren 2002a).

In Sweden, after the first breeding cycle notable improvement in yield has been reached: 10 % at mature age (60 years) for Norway spruce (Westin and Sonesson 2005), 10-25% at age 21-32 years and predicted 20 % at mature age for Scots pine (Rosvall et al. 2002, Ståhl and Jansson 2002, Andersson et al. 2006, Jansson 2007, Jansons et al. 2008), 30% at the age of 30 years for silver birch (Hagqvist and Hahl 1998), 40% predicted at the rotation age at the end of second breeding cycle for coniferous species with shorter rotation period (White et al. 2003). Few of the mentioned studies addressing the predictions of genetic gain have demonstrated that superiority of height growth at juvenile age to be a relatively good predictor for superiority of volume growth at mature age. However, there are no studies addressing this aspect for Norway spruce in Latvia, therefore assumptions of a range of plausible genetic gain values are used in our study rather than a single value.

Considerable decrease in genetic variation have been found between wild population and selected plus trees, but the next steps of selection, based on progeny testing corresponds to only marginal changes in genetic variation (Bouffier et al. 2008). Therefore, it can be assumed that the possibility of further improvement in next breeding cycle remains the same as in the first. Supplemental natural regeneration may reduce the foreseen gain in wood-yield of the improved stands. However, it cannot be considered as an important issue for Norway spruce with flowering periodicity and low survival rate of natural seedlings on open land. Above mentioned arguments as well as field evidence, directly comparing the growth of first generation Norway spruce seed orchard and stands from the same region in Latvia, where difference in yield reached 20% on average (Gailis et al., unpublished), is in line with the estimates used in our study, taking into account that in our study results of second breeding cycle and wild (un-selected) population are compared (Figure 1).

Additional benefits of tree breeding

The financial benefits from tree breeding could be even higher than estimated in our study, since:

1) the management mode in our calculations was not specially adjusted for the improved material. The targeted silvicultural system (Table 3) and optimization of thinning regime considering genotype x management regime interaction (Persson 1994, Dinus and Welt 1995, Lowe et al. 1999, McRae et al. 2004, Roth et al. 2007) can notably increase the revenues from the use of selected material, therefore, also, benefits from breeding process;

2) the improvement in tree quality – branch properties, stem taper, wood properties – that will be achieved with selected material, and therefore higher proportion of high-value assortments, was not considered in our study;

3) the improved material could decrease the production costs for nursery due to more even seedling beds, heavier seeds;

4) the possible failures of natural regeneration – need for supplemental planting or additional early thinning that could increase costs of this method, which we did not consider.

The financial benefit, calculated in our study for Norway spruce is similar to the estimates of Scots pine and silver birch by Ahtikoski (2000). Notably higher benefits can be reached in breeding of fast growing species used in establishment of short-rotation plantations: from 6-8 % (Ledig and Porterfield 1982, Fins and Moore 1984, McKeand et al. 2006) up to 17 % (Talbert et al. 1985).

Tree breeding can be considered also as one of the means of securing wood supply, while increasing areas of forest used for other goals, like infrastructure, recreation, nature protection. From the perspective of state or regional economics, maintaining vital wood processing industry while ensuring source of raw material, could be even more important than the direct economic gain from the increased yield and value of forest stands (Kjær and Foster 1996, Graudal and Kjær 1999).

Tree breeding has a substantial economic role in climate change mitigation, ensuring intensive wood production and carbon binding in high quality wood that will most likely to be used in products with longer life-span. Also selling of CO_2 quotes in international trading schemes can be unimportant as income source from each particular owner but have a substantial economic value at state level (Whittock et al. 2004).

Other considerations

The comparison of the benefit between tree breeding and natural regeneration in our study does not include the analysis of possible consequences to genetic diversity. Direct comparison of trees from 6 randomly selected stands and progenies of 2 seed orchards with 20 and 50 clones, analysed with 6 nuclear SSR markers, for Norway spruce in Latvia revealed that mean number of alleles per locus, observed heterozygosity, diversity index and Shannon's information index as well as number of alleles with frequency ≥5 % did not differ significantly between analysed groups (Jansons et al. 2012). Nevertheless there might be specific cases, e.g. when protection of rare alleles or autochthonous population with specific, genetically determined trait, is of importance, where regeneration with improved material might not be advisable.

The financial revenue from tree breeding also depends on the size of the planting area: the larger the planting area is, the more profitable is the breeding (Tables 3 and 4). This relation is proved to be true also in previous studies dealing with short-rotation coniferous and broad-leaved trees (Ledig and Porterfield 1982, Greaves et al. 2004). To summarise, it indicates, that to be financially profitable, the high-input breeding initiative shall be aimed for a major species with large planting area, such as Norway spruce in most of the northern Europe.

The use of wood prices of one particular year reduces the possibilities to generalize results of our study. However, wood prices used in our study are relatively low; therefore it is unlikely that the benefits from tree breeding would be overestimated due to too high wood prices. Considering the global long-term trends of decrease in forest cover, increase in human population and overall welfare, as well as interest to use more climate-friendly sources of energy and material, increased demand for wood can be predicted (Greaves et al. 2004, Libby 2006). However, increased salaries and costs of forest operations as well as larger areas of plantations of fast-growing woody cultures could level out the possible rise of the benefits for forest owner (Greaves et al. 1997, Sedjo 2001).

The costs of tree breeding are very seldom reflected in the price of improved seed material (Jayawickrama and Carson 2000). Usually it is covered by state or other large-scale forest owners or associations interested in establishment of forests and plantations with trees having certain properties. Therefore, further increase of economic effect from tree breeding can be reached, if the selection is carried out based on selection index, where different properties are combined based on their economic weights (Lowe et al. 1999, Todoroki and Carson 2003). This approach, however, is more appropriate for the selection of species with short rotation, where exact needs of end-user could be predicted with some certainty, since requirements may vary even for different paper producers (Dinus and Welt 1995).

Conclusion

In comparison to natural regeneration, the equivalent annual annuity from Norway spruce breeding is positive from 2.0 to 12.9 EUR ha^{-1}y^{-1}, depending on the breeding strategy, planting area and the silvicultural system. Equivalent annual annuity from the clonal testing is the highest, ranging from 5.5 to 12.9 EUR ha^{-1}y^{-1} and exceeding the other breeding strategies by 34-174 %. Wood prices used in our calculations as well as estimates of testing time and testing size were not inflating the benefit from breeding. Increased use of the improved material together with the targeted silvicultural system in planted stands will further increase the benefits from tree breeding.

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