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Forest Tree Breeding Strategies in Nordic and Baltic Countries and the Possible Implications on Lithuanian Tree Breeding Strategy

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Baliuckas V., Pliūra A., Eriksson G. 2004. Forest Tree Breeding Strategies in Nordic and Baltic Countries and the Possible Implications on Lithuanian Tree Breeding Strategy. *Baltic Forestry*, 10 (1): 95–103.

The forest tree breeding strategies used in Scandinavian and Baltic countries are discussed as regards breeding intensity and breeding systems, methods used for mating, testing, selection, and creation of propagule populations. Types of selection strategies and possible use of genetic estimates for evaluation of gain in tree breeding are discussed. Depending on species, the concepts and methods of tree improvement vary from country to country. First breeding cycle in most countries started with selection of plus trees, generating open pollinated or polycrossed progenies, long-term testing and backward selection. The subsequent breeding cycles or recurrent breeding are based mostly on recombination via open pollination or double-pair mating and on mixed forward selection model under Multiple Breeding Population System or Conventional unstructured system. Implications and options for Lithuanian forest tree breeding activity are presented in the light of this overview. Recurrent long-term breeding combined with gene conservation and based on Multiple Population Breeding System with open pollinated progeny testing would best suit breeding of most forest tree species in Lithuania. More intensive breeding options with double-pair mating can be used for Scots pine and silver birch and in combination with clone tests for Norway spruce. Number of subpopulations, the size of initial material, and intensity of forward selection will be chosen based on the economic importance of each species.

Key words: forest tree breeding, selection intensity, breeding system, selection strategy, genetic gain

Introduction

At present new strategies and programs on breeding and gene conservation of coniferous and broadleaved forest tree species are under preparation, adoption or launched in Lithuania. These programs are of particular importance, as the Program for afforestation of former agricultural lands starting in Lithuania would benefit much from improved plant material. Much can be gained from the analysis from recent development in population and conservation genetics. As funds for forest tree breeding are very limited in Lithuania, sound considerations have to be made as regards strategies, and thereby intensity and methods to be used.

The tree breeding strategies in neighbouring Nordic and Baltic countries are worthwhile to analyse before a strategy for tree breeding is decided upon for Lithuania. Recently such strategies were presented ("Integrating tree breeding and forestry", Proc. of SNS meeting 2001, eds. Haapanen & Mikola). However, the way of presenting the programs varied much among the countries, which complicates a comparison of advantages and disadvantages of the

individual programs. To enable such a comparison it may be useful to try to describe the programs in one uniform way as is done in Figure 1. Four functionally different populations have to be clearly distinguished: breeding population propagule population, production population, and gene resource population. According to Eriksson and Ekberg (2001), breeding population is defined as the collection of trees that will carry the advancement of breeding into future populations, propagule population is the plants or trees utilized in sexual or vegetative propagation, production population is a population intended to produce human utilities, gene resource population is the seeds, acorns, nuts, plants, or trees that are included in the gene conservation. The demand for genetic variability is highest in breeding and gene resource populations.

The management of the breeding population covers three main fields of activities: mating, testing and selection. Each of these activities can be carried out using one out of many alternative methods and that gives a multitude of possible combinations of methods for management of the breeding population.

Intensity of breeding

The intensity of tree breeding varies depending upon the economic importance of each species. The area of forest artificial regeneration in the Scandinavian and Baltic countries varies from 30 to 70 % in general. Coniferous species normally are being regenerated artificially at larger extent than broadleaved trees and mainly with improved seedling material, though the needs for it rarely can be fulfilled at more than 70 percent. As coniferous predominate in forest economy of Scandinavian and Baltic countries, the funds allocated for breeding of coniferous are much larger than the funds allocated for breeding of broadleaved tree species. Tree breeding of coniferous species was traditionally run for many decades, however during the recent decade broadleaved species received more attention.

It is complicated to delimit high and low intensity breeding from each other. Lindgren (2000) described high-intensity breeding as one incorporating full pedigree control (controlled crossings) and genetic testing. Low-intensity breeding is operating with phenotypic selection within progenies raised from background pollination. In breeding there is always a conflict between the demand for gene diversity versus genetic gain. In addition, funding puts a limit to the possibilities of implementation of a desired breeding programme. This conflict was discussed in detail by Lindgren & Karlsson (1993) for Norway spruce breeding in Sweden. The level of genetic variation should be high in production population if natural regeneration of wood producing forest is planned. With short rotation times high genetic gain will be achieved at cost of lesser genetic variation and this restricts the possibility of using natural regeneration, because it could result in inbreeding and decreased sustainability of newly regenerated forests. Implementation of both long- and short- term strategies require educated staff (Lindgren 2000).

Breeding systems

The overview of breeding strategies elaborated in different countries is mainly based on the proceedings from SNS meeting in Finland 2001 (see Fig. 1). At

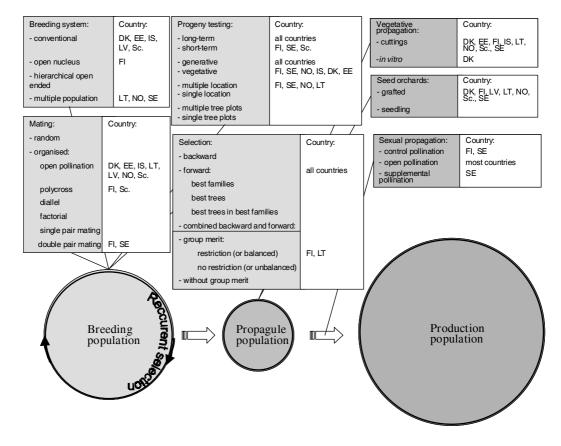


Fig. 1. The principal scheme of forest tree breeding illustrating functionally different populations (modified after Eriksson 2003) and methods of breeding, mating, progeny testing, selection and creating of propagule and production populations used in Scandinavian and Baltic countries. All countries have been listed using international country codes except Scotland, which is indicated by Sc.

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present four main breeding systems can be distinguished: Conventional unstructured (C), Open nucleus (ON), Hierarchical OPen Ended (HOPE) and Multiple Population Breeding System (MPBS). Open nucleus breeding means that the breeding population is split into one small and one large population. The selection intensity is higher in the small population than in the large population, which causes a divergence between the two over time. HOPE means that genes are transferred stepwise via crosses from populations with a low level of improvement to higher levels of improvement. MPBS was first developed by Namkoong (1976). It means that the breeding population is split into approximately 20 subpopulations, each with some 50 genetic entries. Multiple small populations can give greater gains than single populations by selecting and intercrossing among subpopulations. Separate subpopulations can have different breeding goals and traits. Moreover, artificial selection progress rate can vary among subpopulations. The difference from the sublining strategy is that MPBS is aimed at an increase in the among-population additive variance (see Eriksson & Ekberg 2001). It is also advantageous in case of unpredictable global climate warming and changing trait market values (Eriksson et al. 1993; Koski & Tigerstedt 1996). If MPBS is planned for long-term breeding it takes care of gene conservation of the species included in the breeding (cf Eriksson et al. 1993). Thus, MPBS combines the capture of the existing adaptedness while keeping satisfactory additive variance in each subpopulation.

The actual advantageous and disadvantageous aspects of the breeding systems mentioned are also presented in Table 1. One main difference of MPBS from the open nucleus system is that there is no infusion of newly selected material into the breeding population. Such an infusion usually results in reduction of genetic gain. A comparison of the two breeding strategies, MPBS and HOPE reveals that the last one has lower level of genetic diversity (Williams & Hamrick 1995). MPBS prevails in Nordic countries. For a long period a conventional breeding system was dominating in Baltic countries. However, recently in Lithuania, the conventional breeding system is under reorganization into MPBS (Anonymous 2003). Some countries use combinations of different breeding system, eg the Pinus radiata breeding in New Zealand has elements of MPBS, nucleus breeding and sublining (cf. Eriksson & Ekberg 2001).

Mating

Depending on species, the concepts and methods of tree improvement vary from country to country. Although, in the first breeding cycle most countries

Table 1. The main advantages and disadvantages of most common breeding systems used in forest tree breeding. For the explanations of used abbreviations see text above. C= conventional breeding, ON= Open Nucleus system, HOPE= Hierarchial OPen Ended system, MPBS= Multiple Population Breeding System

Breeding systems	Advantages	Disadvantages		
C	Simple to apply in practice	Low level of improvement		
ON	Appropriate level of genetic	Difficult to maintain a large		
	diversity and improvement.	breeding population; possibility to		
		combine with gene conservation		
		is mainly limited to a few forest		
		tree species. At later generations		
		it is less likely that material will		
		be transferred from the large		
		population to the nucleus		
		population owing to the loss in		
		gain connected with such a		
		transfer.		
HOPE	High improvement level in	Comparatively lower genetic		
	elite breeding population.	diversity and difficult to combine		
		with gene conservation.		
		Impossible to use for long-		
		generation time species.		
MPBS	High overall genetic	Many breeding populations have		
	variation and possibility to	to be created.		
	combine with gene			
	conservation in efficient			
	way.			

started with selection of plus trees and open-pollinated or polycrossed progeny in long-term testing followed by mixed forward selection model. This was mainly dependent on the economic importance of the species in the country, geographic peculiarities of the country and national socio-historical heritage. Thus Iceland has the main objective to increase forest area by using proper genetic material. Denmark has very little of indigenous conifer forests and so the efforts are more strengthened on proper choice of seed sources. Openpollinated mating model is being used in most countries except for Sweden and Finland. In Sweden, within each of the unrelated breeding populations, crosses are carried out by means of double-pair mating among 50 members thus securing high genetic variation in next generation.

Progeny testing

Long-term testing is usually applied, which in many cases is combined with medium- or short-term testing since genetic gain per time depends very much

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on the length of the testing period. For most broad-leaved tree species the period of 7-15 years facilitates obtaining efficient breeding with satisfactory juvenile-mature correlations. The choice of single or multiple tree plot testing design is much dependent on testing period and on the number of genetic entries used. Long-term tests and different types of conversions of test trials to other breeding system units would favour multiple plot design. Usually a large number of genotypes and many test localities is associated with single tree plot design, as it is more cost-effective (Osorio et al. 2003).

Testing of generative progenies is often combined with testing of cuttings as clonal testing significantly improves the precision of estimates and generate higher genetic gain (e.g. Burdon 1986, Danusevicius & Lindgren 2001, Danusevicius & Lindgren 2002). However it is suitable only for species that are easy to propagate vegetatively, unless economic interest is very great. Vegetative propagation requires additional funds therefore it can be applied for species that are under high intensity breeding and commonly used in Scandinavian countries. A decade ago an extensive breeding program based on clone testing was run for Norway spruce in Latvia.

Clone testing should be economically well justified, as it requires more resources to be allocated to get final results. It is also assumed that growth performance of clones results in more pronounced G x E interaction compared to half-sib families, so there naturally would be a need to have more testing localities for clone selection. Intuitively, it is logic that progeny testing should be carried out at several test localities to estimate the importance of genotype x environment (G x E) interaction. However, most studies of conifers showed limited importance of G x E (cf. Zhelev et al. 2003), which suggests that the number of test localities could be reduced to what is required from a safety point of view such as loss owing to fire or road constructions or other calamities. McKeand et al. (1990) reported low economic importance of G x E interaction in the test of loblolly pine half-sib families. However, the majority of estimates of G x E refers to individual traits and not to composite traits. Namkoong (1985) and McKeand et al. (1997) reported that a composite trait might show G x E interaction even if the individual components did not show any G x E interaction. These observations call for progeny trials at several localities.

Selection strategies

Forward selection means that the best individuals in a progeny test are selected for seed orchards

and/or subsequent generations of breeding. Backward selection is based on selection of parent trees according to the results from progeny testing. Among-family forward selection followed by within-family selection is mostly used in Scandinavian countries. Dominance of forward selection in breeding programs is reasonable, because it was shown in numerous studies that in most cases forward selection is superior to backward (e.g. Routsalainen & Lindgren 1998). Simulations under considerations of costs, time, genetic parameters and annual budget showed (Danusevicius & Lindgren 2001) that backward selection ("progeny strategy") would yield higher group merit gain per year than forward selection ("phenotype strategy") presumed that sexual maturity is less than 12 years. Group merit gain is expressed as a function (weighed average or index) of its breeding value and gene diversity. There are several strategies of multitrait selection applicable with some modifications if needed which can be recognised as most commonly used for artificial selection on multiple traits. Their main advantages and disadvantages are presented in Table 2. The choice of selection strategy depends on the nature of trait or traits of interest and on the final aim of selection. Study of selection and mating principles by computer simulation (Rosvall and Mullin 2003) revealed that positive assortative mating with selection restrictions on group coancestry enhances gain and also enables to conserve genetic diversity in long-term forest tree

Table 2. The main advantages and disadvantages of most common multitrait selection strategies of forest tree breeding

Selection strategy	Advantages	Disadvantages	
technique involving the	gain in all selected traits in	this strategy, estimates of	
single trait is selected each generation and selection	selection on very different traits (e.g. disease resistance and growth rate); a need to measure only one trait at a time	improvement of several traits;	
independent culling - when any individual not exceeding the preset threshold values in all traits being culled	it can be applied at any time in one generation	large breeding population size is needed to reach the goal; difficult to set appropriate culling levels for each trait, especially when many traits have been selected	

breeding. Fernandez and Toro (2001) have shown that the method of restricted coancestry selection can be effective in cases of strong need to balance expected gain and genetic diversity. The application of this method also does not restrict the larger contribution of the best performing families to the selected group (Lindgren et al. 1989).

Expected genetic gain

The gains that may be obtained from different selection models explicitly discussed by Stern and Hattemer (1964) are summarized in Table 3. The larger the case No, the larger genetic gain would be expected with the largest gains in cases No 5 and 6.

Table 3. Expected genetic gain under different models of selection in forest tree breeding (after Eriksson 1971)

	Mass selection		Type of mating		Type of seed orchard			
Case	Seed	Thinning	Plus	OP^1	Crosses in	Seedling	Clonal	Genetic gain
No	tree		trees		seed			Genetic gain
	stand				orchards			
1.	+	+		+				$h^2 \sigma_p i_i$
2.	+		+	+				$\frac{1}{2}h^2\sigma_{_p}i_{_p}$
3.	+	+	+	+				$\frac{1}{2}h^2\sigma_{_p}(i_{_t}+i_{_p})$
4.			+	+		+		$\frac{1}{2}h^2\sigma_p i_p$
5.			+		+	+		$h^2 \sigma_{_p} i_{_p}$
6.			+		+		+	$h^2 \sigma_{_p} i_{_p}$

¹ OP – open pollinated progeny;

The perspectives for tree breeding, especially for long-term breeding, can be evaluated by using CV, and h_a² estimates. Plotting of narrow sense heritability (h_a²) against additive genetic coefficient of variation (CV_A) estimates in different traits, as shown in Figure 2, can help us indicate the possible selection efficiency, optimise the test period and determine the best traits for selection. This figure is largely based on the data compiled by Hannrup (1999). CV_A is a property of population and is recommended to use as an indicator of long-term potential in any trait of interest (Houle 1992). Large estimate gives an indication of high potential and possibility of high efficiency by breeding. The comparison of CV_A estimates also helps us identify the most diverse populations. High estimate of heritability indicates that short-term testing would be appropriate.

Propagule population

Most breeding programs are closely connected to seed orchard establishment. This synchronization leads to faster use of genetically improved material. Scientifically sound breeding strategy should to some extent guarantee the use of improved genetic resources available in practical forestry and at the same time a guarantee for satisfactory gene conservation. The production population in most countries is formed from material harvested in propagule populations as seed harvested in grafted seed orchards or as cuttings from vegetative propagation, and clonal archives are not used for that purpose, because of larger inbreeding and non-randomised clone distribution in them. Selection strategies for selecting genotypes for creation of propagule populations differ slightly from the selection used in creating breeding populations because usually higher gains are targeted at the cost of lower genetic diversity of reproductive material obtained from seed orchards. An enhanced genetic gain is achieved via increasing intensity of within family selection by means of selecting a smaller number of genotypes and via use of linear deployment strategy (e.g., Wei & Lindgren 1993). Linear deployment means that more selections are being made in families having larger breeding value.

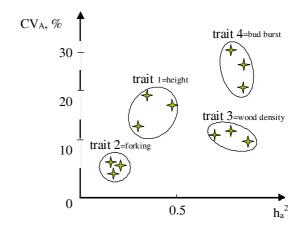


Figure 2. Plotting of theoretically possible population estimates (indicated by stars) of heritability (h_a^2) against additive genetic coefficient of variation (CV_A) in different traits of interest for tree breeding in forest tree species

Considerations for forest tree breeding in Lithuania

Before options for a breeding strategy for Lithuania is discussed, it is important to mention that it would be economically advantageous if the breeding methods suggested incorporate gene conservation. In

 h^2 =heritability; σ_p =phenotypic standard deviation; i_i =selection intensity at thinning (female tree selection); i_p =plus tree selection intensity.

agreement with Eriksson (2001) we have safeguarding of the potential for adaptation as the prime objective of gene conservation. The main choice is to select among the breeding systems presented in Table 1. To identify the breeding strategy that matches the breeding objectives we need to know the background information on species and traits of interest, that is: genetic variation within- and among- populations, species life history characteristics, evolutionary pathways, life-history tradeoffs, and perspectives of adaptation and performance under global climatic change. The evidence of differences in species characteristics indicates that breeding strategies may differ as well for separate species or group of species. The decision needs to be taken on breeding objectives, founder population(s) size, selection intensity, breeding cycles planned, selection strategies and their modes.

Pliura and Eriksson (1997) argued that Scots pine breeding in Lithuania might have the same breeding strategy as Scots pine in Sweden. This strategy is based on high-intensity Multiple Population Breeding System, which integrates ex-situ conservation of forest genetic resources. It also matches the prime objective of gene conservation. We consider that the intensity of selection in Swedish breeding programs is optimal as regards the balance between genetic gain and genetic variation in comparison to aggressive tree breeding carried out in US or to mild selection intensity of extensive tree breeding program in Finland. Up to now, the running breeding program for conifers in Lithuania has intermediate intensity with genetic tests of open pollinated families at several locations and forward selection between and within families. It is closely connected to the establishment of the second-generation seed orchards. This breeding strategy seems to fulfil the requirements of long-term breeding and can be efficiently connected to dynamic gene conservation for most broadleaved species in Lithuania (Baliuckas & Pliura 1998). The linear deployment strategy was already applied in Lithuania for Scots pine and Norway spruce for selection of material for establishment of the second-generation seed orchards based on open-pollinated progeny trial information (project "Selection of open-pollinated families and female trees of Scots pine and Norway spruce by forest natural regions for the second cycle seed orchards", leader A. Pliura). The mixed forward and backward (for the part of the top ranking families) selection scheme was used in order to obtain as much genetic improvement as possible while keeping relatively high genetic variation.

At present the MPBS concept with establishment of at least one progeny trial - *ex-situ* breeding population with 50 genetic entries in each of the adaptive environments (breeding zones/provenance regions) is

widely accepted in Lithuania (Baliuckas & Pliura 1998, Gabrilavičius & Danusevičius 2003). Nevertheless, it is still sometimes argued in favour (Gabrilavičius, Danusevičius 2003) to use provenance trials for breeding of conifers in Lithuania. According to Eriksson and Ekberg (2001) provenance trials have two main objectives (1) to identify the best seed source, (2) to give information on the past evolution of the species. Provenance information can be used to identify the provenance to use for selection of material for the founder population in breeding. If the breeding program is based initially on provenance experimental trials only, it restricts the application of MPBS in breeding programs. It is not able to generate significant genetic gain and does not contribute to dynamic gene conservation (cf Varela and Eriksson 1995 for a discussion of merits of different genetic entries in gene conservation). Koski (1997) in his paper on national strategy of gene conservation stressed that in terms of long time breeding populations the concurrent provenance trials and clonal collections are a blind end. In conclusion the existing provenance trials and clonal archives can be used in breeding programs, but to a very limited extent, e.g. for generating data which can be used as initial information for further use of seed sources and for yielding a complementary reproductive material for forest regeneration in case there is a lack of reproductive material from seed orchards.

Most published experimental results on forest tree breeding show that full-sib tests are reliable and predictable by giving similar estimates of age-age correlation or genetic correlations of the same traits across sites (Dieters et al. 1995). However, the cost of full-sib tests is too high to allow an application of them under current economic situation in Lithuania. The established open-pollinated progeny trials with sufficient number of families per population serve as a good compromise between genetic information and economic input. Moreover, such an approach satisfies future breeding needs and dynamic gene conservation. As relatedness and gain are the major outcomes of breeding the first one could be successfully solved by using halfsib families, simply assuming that half-sib families have four times the effective size or status number as clones from the same plus tree (Lindgren et al. 1996, Lindgren 2000). Recurrent long-term breeding combined with gene conservation and based on Multiple Population Breeding System with recurrent cycles of recombination and generating open-pollinated progeny within each breeding subpopulation, medium-term testing in network of progeny trials in different provenance regions and within-family forward selection would best suit most forest tree species in Lithuania. More intensive breeding options with double-pair mating can be used for

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Scots pine and silver birch and in combination with clone tests for Norway spruce. Number of subpopulations, the size of the initial material, and the intensity of forward selection would be chosen based on the economic importance of each species. The economic importance of native forest tree species is presented in Table 4. Pinus sylvestris and Picea abies, up to 12 (2 in each provenance region) ex situ breeding populations would be reasonable to create, for Betula pendula, Quercus robur, Alnus glutinosa, Populus tremula and Fraxinus excelsior up to 5-6 (1-2 in each provenance region), for Acer platanoides and Tilia cordata up to 3-4 populations, and for each of the rarely occurring species 1 collection/gene conservation population would be sufficient. The national program for forest tree gene conservation and breeding development for 10year period (2004-2013) was adopted at Ministry level in 2003 (Anonymous 2003). Tree breeding measures, methods, intensity, and funds allocated were assigned separately to conifers and deciduous tree species. This policy was based on already achieved improvement in conifer breeding and the urgent needs to speed up a

Table 4. The occurrence, population size and economic importance of native forest tree species (which could be regarded as suitable for breeding) arranged by their stands area. The more 'plus' signs the greater the economic importance.

Species	Occurrence	Population size	Economic importance
Pinus sylvestris	widely occurring	average to large	+++
Picea abies	widely occurring	average to large	+++
Betula pendula	widely occurring	large	+++
Alnus incana	widely occurring	average to large	+-
	(C-N Lithuania)		
Alnus glutinosa	widely occurring	average to large	++
Populus tremula	widely occurring	average to large	+
Betula pubescens	widely occurring	average to large	+
Fraxinus excelsior	widely occurring	small to average	+
Quercus robur	widely occurring	small to average	++
Carpinus betulus	scattered occurrence	small to average	-
	(S-SW Lithuania)		
Tilia cordata	scattered occurrence	small	+-
Ulmus glabra	scattered occurrence	small	+-
Ulmus laevis	scattered occurrence	small	+-
Acer platanoides	scattered occurrence	small	+-
Larix decidua	scattered occurrence	small	+-
Fagus sylvatica	rarely occurring	small	-
	(SW Lithuania)		
Quercus petraea	rarely occurring	small	+-
	(S Lithuania)		
Pyrus communis	rarely occurring	small	-
Prunus avium	rarely occurring	small	-
	(W-SW Lithuania)		

tree breeding of deciduous tree species. Gene conservation and long-term tree breeding are jointly incorporated into this program. There are no native forest tree species in Lithuania that should be preserved at species level, so long-term breeding and gene conservation can be successfully applied as a joint action.

Based on the discussion above, the existing and planned breeding methods for the breeding of different forest tree species in Lithuania are summarised in Figure 3 (see page 102).

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Figure 3. The principal scheme of forest tree breeding illustrating functionally different populations (modified after Eriksson 2003) and methods of breeding, mating, progeny testing, selection and creating of propagule and production populations being used for the breeding of different forest tree species in Lithuania.

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СТРАТЕГИИ СЕЛЕКЦИИ ЛЕСНЫХ ДРЕВЕСНЫХ ПОРОД В СКАНДИНАВСКИХ И БАЛТИЙСКИХ СТРАНАХ И ИХ ЗНАЧЕНИЕ ДЛЯ СТРАТЕГИИ СЕЛЕКЦИИ В ЛИТВЕ

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Резюме

Существующие в Скандинавских и Балтийских странах стратегии селекции лесных древесных пород представлены в аспектах интенсивности и системы селекции, методов скрещивания, тестирования, отбора и создания популяции размножения. В статье обсуждаются типы стратегий выбора и возможного использования генетических оценок для определении выгоды в селекции древесных пород. В зависимости от разновидностей, понятия и методы селекции древесных пород различаются в разных странах. Первый цикл селекции в большинстве стран начался с выбора плюсовых деревьев, производя потомство путём открытого опыления или поликроса, используя долгосрочные испытания и назад обращённый отбор. Последующие циклы селекции или текущая селекция проводится главным образом через рекомбинации путём открытого опыления или скрещивания двойной пары и на смешанной вперёд направленной модели отбора под Многократной Популяционной Системой Селекции или Обычной неструктурированной системой.

В свете этого краткого обзора представлено значение и возможные варианты селекции лесных древесных пород в Литве. Текущяя долгосрочная селекция, объединенная с сохранением генетических ресурсов и основанна на Многократной Популяционной Системе Селекции с испытанием потомства полученного путём открытого опыления лучше всего подошло бы для селекции большинства лесных древесных пород в Литве. Более интенсивные варианты селекции со скрещиванием двойной пары могут использоваться для сосны обыкновенной и березы бородавчатой и, в комбинации с испытаниями клонов, ели обыкновенной. Число субпопуляций, объём начального материала, и интенсивность вперёд направленной селекции будет подобрано для каждой породы на основе её экономической важности.

Ключевые слова: селекция лесных древесных пород, интенсивность отбора, система селекции, стратегия отбора, генетическая выгода