Genetic Variation in Adaptive Traits of Progenies of Lithuanian and Western European Populations of *Fraxinus excelsior* L.

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Abstract

The study aimed at evaluating genetic features of populations and genetic variation of adaptive traits and RAPD markers of open pollination progenies from Lithuanian and western European populations of *Fraxinus excelsior* in field trials, established in three different provenance regions of Lithuania. Progenies of the Lithuanian populations had earlier bud flushing and better health condition than the progenies of western European populations in all three trials, but tree height was smaller (except the Šilutė population). Genetic effects at population and family levels were significant for all traits studied. Although family variance component was not high reaching from 11.6 to 22.6%, the additive coefficient of genetic variation was high ranging from 30.3 to 36.8% in separate field trials. Genetic variation of adaptive traits and RAPD markers did not correlate in most populations, thus indicating its differing adaptive potential. The Šakiai and Kupiškis populations had high genetic variation of both in adaptive traits and in RAPD markers, while other populations had differing levels of genetic variation in RAPDs and adaptive traits. The genetic changes within population variation across sites were population specific. Such changes can alter adaptation, stability, and competitive ability of newly formed populations in a hardly predictive way.

Key words: populations, progeny, half-sib families, genetic variation, adaptive traits, genotype × environment interaction

Introduction

Recent changes in climate and the environment and increased amplitude of fluctuation increase pressure on forest tree populations that have been establishing themselves during centuries under comparative slow natural changes of the environment. This strong pressure generates not only the physiological response of trees, however it also causes genetic changes through intensifying natural selection. Genetic variation of growth rhythm traits is the main prerequisite for adaptation to changing environment (Ekberg *et al.* 1982, 1985, Skrøppa 1982, Ståhl 1984). The time of seasonal growth initiation, length of growth period and time of growth cessation have become strongly genetically determined in the course of evolution through adaptation to specific thermo- and photo-period along latitudinal and altitudinal gradients (Ekberg *et al.* 1979, Dormling 1979, Sundblad, Andersson 1995, Aķo 1994, Jonsson *et al.* 1981). Wide range of species distribution and huge diversity of environment conditions facilitate climatic and edaphic differentiation of populations. This in combination with small isolated populations causes large genetic variation (Weisgerber 1974). Postglacial migration of forest trees from glacial refuge areas in South Europe had also influenced the among-population variation, structure of populations, and genetic diversity within populations. Disruptive and directional natural selection, gene flow and mutations continue to shape population structure and patterns of genetic variation (Eriksson and Ekberg 2001). In addition to these natural factors, human activity also influences genetic differentiation of forest tree species (Wang Xiao-Ru *et al.* 2001).

Significant differences among some provenances/populations of *Fraxinus excelsior* have been found at phenotypical level as well as in progeny testing (Nikolaeva and Vorob'eva 1978, Smintina 1993, Giertych 1995a, 1995b, Kleinschmit 1994, Kleinschmit *et al.* 1996, *etc.*). However, extensive studies of intra-population geographical variation based on the progeny testing were performed only for American species of *Fraxinus* (Clausen *et al.* 1981, Clausen 1984, Raymond and Lindgren 1990, Roberds *et al.* 1990, Schuler 1994, *etc.*). The present scattered distribution and specific ecological requirements indicate that populations of

Fraxinus are probably more differentiated than those of wind pollinated species with continuous distribution. Studies of DNA markers indicated that genetic differences among populations of *Fraxinus excelsior* were more pronounced within than among oak populations (Heuertz *et al.* 2001). As many broadleaved forest tree species occupy a great variety of sites, many studies in the former Soviet Union and other East European countries were oriented towards investigation of ecotypes and diversity of forms (Любавская 1982, Shutyaev 1986, Paule, Yazdani 1992). Many phenological, morphological, edaphic, and other forms have been described. However, the existence of ecotypes has not been proven in experimental field tests and therefore postulated soil races or ecotypes should be considered as being phenotypic (Weiser 1995). Results from half-sib progeny trials have shown the existence of significant within-population variation as well. In most experiments a variation between single-tree progenies between families within provenances was as high as the variation between provenances (*e.g.*, Baliuckas *et al.* 1999, 2000, Baliuckas 2002).

Studies of broad-leaved tree species have shown that genetic variation and heritabiliy of adaptive traits differ in different environmental conditions of progeny testing (Baliuckas, Pliūra 1999, 2000, 2003, Baliuckas *et al.* 1999, 2000, 2001, Pliūra, Eriksson 2002, Pliūra, Kundrotas 2002, Pliūra 2004, Lauteri *et al.* 2004). Comparative studies of broad-leaved tree species have approved the hypothesis that climax tree species might have larger genetic variation within populations than that of pioneer tree species, however this was true only for bud flushing phenology (Baliuckas 2002). It has been found that frost resistance, growth, and stem quality depend to the great extent on bud flushing and bud set phenology (*e.g.*, Baliuckas, Pliūra 1999, 2000, 2003, Pliūra, Kundrotas 2002).

The survival of forest tree populations and species under rapid changes of climate and the environment will depend both on physiological and genetic adaptation. The potential for genetic adaptation to the greatest extend depend on existing among- and within-population genetic variation of adaptive traits. During recent decade the greatest part of ash stands in Lithuania was lost because of ash dieback (Juodvalkis, Vasiliauskas 2002). The health condition of survived stands remains poor. In 2006, the outbreaks of ash dieback were still present on 9.4 thousand hectares, despite extensive clear cuts of severely damaged stands (Lithuanian Statistical Yearbook of Forestry, 2006). The main reasons for ash dieback remain unclear, however most of damages can be attributed to outbreak of diseases (*e.g.*, *phytoplasma*, *mycoplasma, phytophtora, etc.*), which is related to changes in the environment and climate and the emergence of new pathogens and their vectors (insects) in Lithuanian forests. The studies of DNA chloroplast markers have shown that only one haplotype group has reached Lithuania after postglacial migration from a refuge in Balkans (Heuertz *et al.* 2003), thus genetic variation probably is rather limited. The lack of resistance to disease might be specific to this branch of postglacial migration or can be attributed to low genetic variation. However, up till now information on the genetic variation of adaptive traits in Lithuanian populations of *Fraxinus excelsior* is missing. In 2001, at the beginning of severe ash dieback, the extensive sampling of seed from Lithuanian populations of *Fraxinus excelsior* was undertaken in order to collect genetic material for gene conservation purposes and progeny studies. Additionally to this, the seed samples were exchanged with many European partners to increase genetic variation of *Fraxinus excelsior* in order to enhance the adaptive potential to fight the ash dieback. In 2005, the series of progeny field trials consisting of 3 large trials have been established in 3 provenance regions of Lithuania in addition to 6 progeny trials recently established in Western Europe. This was aimed to collect and conserve the diverse genetic resources of *Fraxinus excelsior*, to study genetic features and genetic variation, and to perform practical tree breeding. The information on genetic variation of adaptive traits is urgently needed to prepare the program for tree breeding, gene conservation, and restoration of ash stands.

The aim of this study was to estimate genetic features of populations and intra- and inter-population genetic variation of adaptive traits in comparison with RAPD markers of open pollination progenies from Lithuanian and western European populations of *Fraxinus excelsior* in three field trials, established in different provenance regions of Lithuania.

Material and methods

Material

Material consisted of 140 open pollination families from 10 Lithuanian populations and 180 open pollination families from 14 western European populations (Table 1, Fig. 1). Seed samples from western European populations of *Fraxinus excelsior* were provided by partners from EC FP6 project "RAP: Realizing Ash's Potential". Each population is represented by a half-sib progeny from 10 to 30 seed trees sampled in natural stands of *Fraxinus excelsior.* Minimum distance between sampled trees was 50 m to avoid relatedness. Seedlings were raised in nursery for 3 years and then transplanted to three progeny trials

located in Telšiai, Pakruojis, and Kėdainiai forest enterprises in different adaptive environments, 1st, 2nd, and 4th provenance regions of *Fraxinus excelsior* (Table 2, Fig. 1). Each progeny trial was established in a randomized complete block design, with 6 blocks consisting of 5 to 7 single-tree plots of each family in each block. Totally over 9000 trees planted in each progeny trial. Trees were planted in rows, 2.5 m between rows, 1.5 m between trees.

Table 1. Number of families in populations and geographical data of their origin

Population	Number of families	N. Latitude	Longitude	Altitude m a.s.l.
Lithuanian:				
Šakiai, LT	10	55°01′	23°05′E	59
Šilutė, LT	10	55°15′	21°42′E	16
Telšiai, LT	10	56°04′	22°27′E	138
Marijampolė, LT	10	54°26′	23°27′E	119
Kaišiadorys, LT	30	54°53′	24°22′E	89
Pakruojis, LT	30	56°17′	24°03′E	39
Ignalina, LT	10	55°16′	26°33′E	137
Nemenčinė, LT	10	54°59′	25°30′E	163
Kupiškis, LT	10	55°51′	25°10′E	97
Kėdainiai, LT	10	55°11′	24°00′E	67
West European:				
t'Hoge Bos, BE	13	50°50′	2°57′E	60
Currachase, IE	20	52°36′	8°53′W	30
Donadea, IE	20	53°20′	6°45′W	92
Enniskillen, IE	20	54°14′	7°28′W	45
Breg.Ost.Rav,D	*	55°17′	9°32′E	38
Farchau, DE	15	53°44′	10°43′E	38
Haguenau, FR	17	48°49′	7°47′E	117
Monterolier, FR	18	49°38′	1°21′E	190
Morscwiller, FR	19	47°42′	7°16′E	280
Val.Saint.Pier.FR	20	49°47′	3°54′E	180
Rabstejn, CZ	16	49°56′	17°15′E	800
Sczceciniek, PL	*	53°42′	16°41′E	150
Mircze, PL	*	50°38′	23°55′E	220

* - mixture of population seeds was used

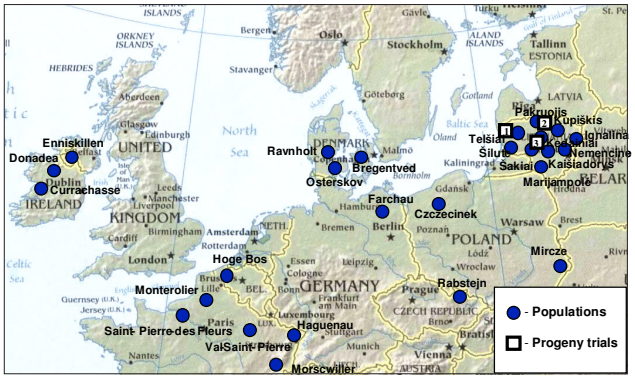

Figure 1. Sampled western European and Lithuanian populations of *Fraxinus excelsior* and progeny field trials established in Lithuania

Table 2. Main characteristics of three Lithuanian *Fraxinus excelsior* progeny field trials of 2005-year trial series

No.	Progeny trial (Forest enterprise, forest district)	Area, ha	Latitude N	Longitude E	Altitude a.s.l., m	Provenance region	Index of continentality.	Site index
1	Telšiai, Ubiškiai	3.0	56°03′	22°25′	147	1	Marit.-25	Ld
2	Pakruojis, Žeimelis	3.0	56°14′	23°53′	53	2	Transit.-28	Ld
3	Kėdainiai, Labūnava	2.5	55°25′	24°19′	54	4	Transit.-28	Ld

Measurements

Tree height was measured and bud flushing class (from 1 – late flushing to 5 – early flushing) was recorded for each seedling at 3 years of age in nursery before transplanting to field trials. In each progeny field trial at age 4 years (spring 2006), bud flushing class and tree health condition (from 1 – dead dry tree to 5 – completely healthy tree) was recorded.

Statistical analysis

Variance analysis was done using the MIXED procedure in SAS Software (SAS Institute, Inc., SAS/STAT software Release 8). Mixed model equations (MME) and the restricted maximum likelihood (REML) method were used to estimate the significance of effects of different factors and to compute variance components of random effects. *F* tests were carried out to determine where fixed effects were significantly different from zero. The significance of random effects was tested with the *Z* test. The following linear model was used for joint analysis of data from all three progeny field trials together (1):

$$y_{ijlmnn} = \mu + z_i + b_j + s(p)_{lm} + p_m + pz_{mi} + s(p)z_{lmi} + e_{ijlmn}$$

where y_{ijlmn} is an observation of the *n*-th tree from the *l*-th family in the *m*-th population in the -th progeny field trial, μ is the overall mean, Z_i is the fixed effect due to the -th progeny field trial, b_j is the effect of *j*-th block, $s(p)_{lm}$ is the random effect of the *l*-th family in the *m*-th population, p_m is the fixed effect of the *m*-th population, pz_{mi} is the fixed effect of interaction between the *j*-th population and the -th field trial, $s(p)z_{lmi}$ is the random effect of interaction between the *l*-th family in *m*-th population and *i*-th field trial, e_{ijlmn} is the random residuals. The model assumes that the random effects are normally distributed with expectation zero and corresponding variances σ_s^2 and σ_{sz}^2.

The following linear model was used for separate analysis of data in each individual progeny field trial (2):

$$y_{jlmn} = \mu + b_j + p_m + s(p)_{lm} + pb_{mj} + s(p)b_{lmj} + \varepsilon_{jlmn}$$

where y_{jlmn} is an observation on the *n*-th tree from the *l*-th family in the *m*-th population, μ is the field trial mean, b_j is the fixed effect of *j*-th block, p_m is the fixed effect of the *m*-th population, $s(p)_{lm}$ is the random effect of the *l*-th family in the *m*-th population, pb_{mj} is the fixed effect of interaction between the *m*-th population and the *j*-th block, $s(p)b_{lmj}$ is the random effect of interaction between the *l*-th family in *m*-th population and *j*-th block, ε_{jlmn} refers to the random residuals. The model assumes that the random effects are normally distributed with expectation zero and corresponding variances σ_s^2 and σ_{sb}^2.

Estimates of genetic parameters

Genetic parameters and their standard errors were estimated using variances and covariances obtained from the SAS Mixed procedure. Genetic parameters were estimated both for each progeny field trial and for each population in each individual field trial. The variance components of random effects of families, interaction between family and field trial, and interaction between family and block were computed from the corresponding variances and expressed in percent of the total random variation, *e.g.*,

$$vc_s = \sigma_s^2 /(\sigma_s^2 + \sigma_{s*b}^2 + \sigma_e^2) * 100$$

where vc_s is the variance component of families, σ_s^2 is the family variance, σ_{s*b}^2 is the variance of interaction between families and blocks, σ_e^2 is the variance of random residuals.

The additive coefficient of genetic variation was calculated for each individual field trial and for each population in each field trial using the formula:

$$CV_A = \sqrt{4 \cdot \sigma_s^2} \cdot 100 / \overline{X}$$

where σ_s^2 is the family variance in field trial or in each population respectively, $\overline{X}$ is the phenotypic mean in the trial or phenotypic mean of population respectively.

The additive variance for half sib families was estimated as (Falconer 1989):

$$\sigma_a^2 = 4 \cdot \sigma_s^2$$

where σ_a^2 is the additive variance, σ_s^2 is the family variance.

The heritability coefficients were estimated as:

$$h_a^2 = \sigma_a^2 / \sigma_f^2$$

where h_a^2 is the heritability coefficients, σ_a^2 σ_f^2 is the phenotypic variance:

$$\sigma_f^2 = (\sigma_s^2 + \sigma_e^2),$$

where σ_s^2 is the family variance, σ_e^2 is the variance of random residuals.

The standard errors for heritability were obtained as follows (Swiger *et al.* 1964):

$$se = 4 \cdot \sqrt{\frac{2 \cdot (n-1) \cdot \left[1 + (k-1) \cdot \left(\frac{h_a^2}{4}\right)\right]^2 \cdot \left(1 - \left(\frac{h_a^2}{4}\right)\right)^2}{k^2 \cdot (n-N) \cdot (N-1)}}$$

where n is the total number of individual values, N - the number of families, k - harmonic mean of observations per family.

Estimated parameters of genetic variation of adaptive traits were analysed and compared to parameters of genetic variation of RAPD DNA markers presented in previous study (Žvingila *et al.* 2005): observed number and percentage of polymorphic RAPD bands, the Shannon index, mean genetic distance among individuals in population, and intra- and inter-population variance components. Methods and software used in estimating these parameters are described in detail by Žvingila *et al.* (2005).

Results and discussion

Joint analysis of all field experiments using model 1 (see M&M) revealed the significance of genetic factors –within populations and families in variation of adaptive traits among the ash progeny (Table 3). The percentage family variance component from total phenotypic variation was quite small and varied from 2.4 to 11.5%. Bud flushing and tree health condition family variance components varied from 11.6 to 22.6%

Effect	df.	Bud flushing phenology			Tree health condition			Tree height		
		Variance component ±st. error,%	*Z* or *F*	Probability	Variance component ±st. error, %	*Z* or *F*	Probability	Variance component ±st. error, %	*Z* or *F*	Probability
Families	315	2.4 ±0.43	5.5	<0.001	2.6 ±0.42	6.2	<0.001	11.5 ±1.21	9.5	<0.001
Populations	21		46.2	<0.001		51.3	<0.001		18.6	<0.001
Sites	2		653.1	<0.001		922.4	<0.001			
Blocks	12		115.4	<0.001		40.1	<0.001		29.9	<0.001
Family x trial interaction	704	2.5 ±0.43	5.8	<0.001	1.5 ±0.37	4.1	<0.001			
Population x trial interaction	42		4.67	<0.001		3.9	<0.001			
Error	19144		95.4	<0.001		95.4	<0.001		68.2	<0.001

Table 3. Results from joint mixed linear model analysis of variance of bud flushing phenology, tree health condition of progenies from western European and Lithuanian populations of *Fraxinus excelsior* at three progeny trials combined and of tree height in nursery trial: variance components and their standard errors for random effects as percent of the total random variation, Z-criteria and probability of effects, *F*-criteria and probability for fixed effects

at each separate field trial (Table 4). Additive genetic coefficients of variation (CV_A) for adaptive traits were relatively high reaching in some trials up to 36.8% (Table 4). That indicates the existence of pronounced genetic differences between families. So, the material studied can serve as a good basis for gene conservation and practical tree breeding.

Table 4. Results from the mixed linear model (2) analysis of bud flushing phenology and tree health condition of progenies from western European and Lithuanian populations of *Fraxinus excelsior* in three progeny field trials: trial means, family variance components as percent of the total random variation, its standard errors, heritability, and genetic coefficient of additive variation (CV_A)

Field trial	Bud flushing phenology				Tree health condition			
	Mean, class	Family variance component ±std. error, %	Heritability ±std. error	CV_A, %	Mean, class	Family variance component ±std. error, %	Heritability ±std. error	CV_A, %
Kėdainiai	3.04	19.7 ±2.1	0.79 ±0.06	36.2	3.24	22.6 ±2.2	0.91 ±0.07	36.2
Pakruojis	1.98	11.6 ±1.4	0.47 ±0.05	30.3	2.02	13.0 ±1.5	0.52 ±0.05	36.8
Telšiai	2.55	15.4 ±1.7	0.62 ±0.05	35.1	2.96	13.9 ±1.6	0.55 ±0.05	30.9

Population effect for all adaptive traits studied was strongly significant (P<0.001, Table 3). Population effect was considered as fixed and, due to that, variance component for population was not calculated. On the other hand, high estimate of the Fisher criteria let us suppose that population structure (differences between populations) is strongly expressed (Table 3). Studies of chloroplast DNA based on microsatellites and PCR-RFLP suggest that the geographical pattern displayed by the five most common haplotype lineages with high among population differentiation (G_{ST} = 0.89), reflecting poor mixing among recolonising lineages (Heuertz *et al.* 2004a). Two populations of the present study, namely from Pakruojis and Kaišiadorys, belong to the same migration lineage (group). It is likely that all natural ash populations in Lithuania are from the same lineage.

Recent studies of molecular RAPD markers of 10 Lithuanian populations have shown that only 8.3% of the total genetic variation was within populations (Zvingila *et al.* 2005). This reveals rather pronounced genetic differentiation between populations. Comparative RAPD marker studies of 3 Lithuanian and 5 Polish populations have also suggested relatively high population differentiation (Nowakowska *et al.* 2004). Recent nuclear microsatellite studies of *Fraxinus excelsior* in Europe show that Lithuanian populations belong to a large deme that occupy the area from British Isles to central-east Europe and is of very homogenous genetic structure with less population differentiation than in southeast Europe (Heuertz *et al.* 2004b).

Progenies of the Marijampolė, Kaišiadorys, Ignalina, and Nemenčinė populations were the earliest in bud flushing among Lithuanian populations in all three progeny field trials (Table 5). Tree condition in two of these populations, Marijampolė and Ignalina, was the best in all trials. The Kupiškis and Šilutė populations were late flushing ones. The bud flushing of progenies from all western European populations occurred later (low bud flushing class) than that in progenies of Lithuanian populations (higher bud flushing class, Fig. 2). The bud flushing time of the earliest flushing French populations Morscwiller and Val-Saint-Pierre and Czech population Rabstejn was close to the average bud flushing time of progenies of Lithuanian populations. All three Irish populations were the latest flushing in all progeny field trials. The correlation between bud flushing and tree condition of populations (Lithuanian and western European) was positive and strong (r = 0.81, 0.78, and 0.92 in the Kėdainiai, Pakruojis and Telšiai field trials, respectively), indicating that earlier flushing populations have better tree health condition. This finding does not correspond to the results from earlier studies of Swedish populations of *Fraxinus excelsior* where earlier bud flushing trees were more severely damaged by spring frost (Baliuckas *et al.* 1999). However, the character of this relationship depends to a great extent on the time (date) of occurrence of spring frost in relation to the bud flushing time and varies greatly year-to-year. Distance from location of population origin to Kėdainiai trial, where bud flushing and health showed highest variability, strongly correlated with those traits at population level. Spearman correlation was -0.83 and -0.84 correspondingly, meaning that earlier flushing populations originated from the higher latitudes and larger longitudes. Correlation value for latitudinal difference was almost twice as less as for longitudinal one for bud flushing and this result much depends on the population origin pattern (see Fig. 1).

Progenies from the Šilutė, Šakiai and Telšiai populations were interior by growth (Figure 3). Best tree health condition of progenies in all three trials was

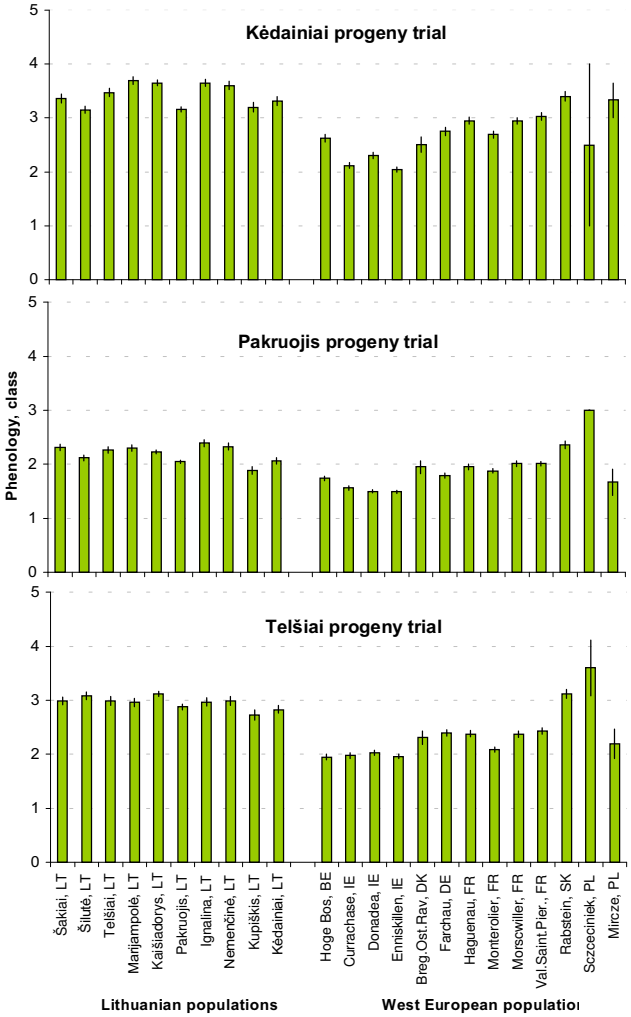

Figure 2. Bud flushing phenology of progenies from Lithuanian and western European populations of *Fraxinus excelsior* in Kėdainiai, Pakruojis, and Telšiai progeny field trials (pins on top of bars indicate standard errors of populations means)

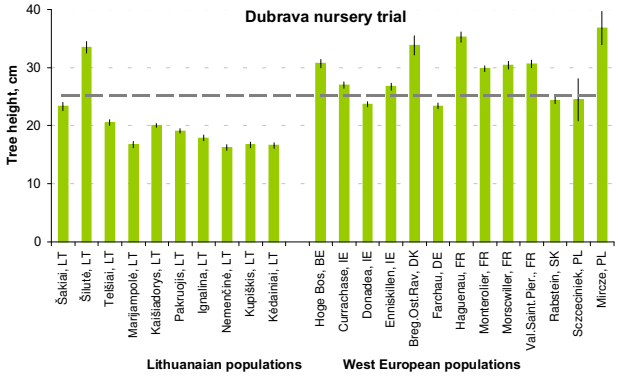

Figure 3. Height growth of progenies from Lithuanian and western European populations of *Fraxinus excelsior* in nursery trial before transplanting to three progeny field trials (pins above bars indicate standard errors of populations means, horizontal dashed line indicates trial mean)

characteristic of the Marijampolė, Ignalina, and Kėdainiai populations (Table 5, Fig. 4). Heavy one-year spring frost at the Pakruojis site caused damage of leaves and flushing buds and, as a consequence, tree health condition in general was there worst of all trials studied. Health condition of all Lithuanian progenies in all three trials was better than of the western European ones. The Farchau population progenies from Germany, the Rabstejn – from Czechia and the Sczceciniek – from Poland were the healthiest among the foreign progeny (Table 5). All mentioned populations are also among the geographically closest to Lithuania. Although, best growing populations were from Poland and Denmark. Progenies of the Lithuanian populations, except the Šilutės population, had smaller height than progenies of the western European populations (Fig.4). This corresponds to the results from earlier studies of Swedish populations of *Fraxinus excelsior* that have

Table 5. Tree height, bud flushing phenology and tree health condition of western European and Lithuanian populations of *Fraxinus excelsior* in three progeny field trials

Populations, country	Number of trees in trial	Nursery trial		Kėdainiai field trial				Pakruojis field trial				Telšiai field trial			
		Tree height, cm		Phenology, class		Condition, class		Phenology, class		Condition, class		Phenology, class		Condition, class	
		Mean	±std.er.	Mean.	±std.er.	Mean	±std.er.	Mean	±std.er.	Mean	±std.er.	Mean	±std.er.	Mean	±std.er.
Lithuanian:															
Šakiai, LT	236	**23.34**	±0.70	3.36	±0.08	3.74	±0.07	2.31	±0.06	2.22	±0.06	2.99	±0.07	3.48	±0.08
Šilutė, LT	297	**33.48**	±1.01	3.15	±0.07	3.43	±0.06	2.12	±0.05	2.15	±0.06	3.09	±0.07	3.43	±0.07
Telšiai, LT	268	**20.54**	±0.51	3.47	±0.08	3.75	±0.08	2.26	±0.06	2.31	±0.07	2.99	±0.08	3.35	±0.07
Marijampolė, LT	229	16.78	±0.55	3.69	±0.07	**4.05**	±0.07	2.30	±0.06	**2.56**	±0.08	2.96	±0.08	**3.48**	±0.08
Kaišiadorys, LT	612	20.03	±0.36	3.65	±0.05	3.82	±0.05	2.23	±0.04	2.30	±0.04	3.12	±0.05	3.45	±0.05
Pakruojis, LT	681	19.08	±0.37	3.16	±0.05	3.80	±0.05	2.05	±0.03	2.34	±0.04	2.88	±0.05	3.44	±0.05
Ignalina, LT	249	17.89	±0.51	3.65	±0.07	**4.05**	±0.07	2.39	±0.06	**2.53**	±0.07	2.97	±0.08	**3.50**	±0.08
Nemenčinė, LT	205	16.21	±0.49	3.60	±0.08	3.87	±0.08	2.33	±0.06	2.53	±0.07	2.99	±0.08	3.48	±0.08
Kupiškis, LT	192	16.71	±0.48	3.20	±0.09	3.56	±0.10	1.89	±0.07	2.22	±0.09	2.73	±0.09	3.24	±0.10
Kėdainiai, LT	225	16.61	±0.48	3.31	±0.08	**4.03**	±0.07	2.06	±0.06	**2.64**	±0.08	2.83	±0.07	**3.53**	±0.08
West European:															
Hoge Bos, BE	267	30.69	±0.68	2.62	±0.07	2.60	±0.06	1.74	±0.04	1.68	±0.05	1.95	±0.05	2.46	±0.06
Currachase, IE	300	27.00	±0.57	2.12	±0.05	2.68	±0.06	1.56	±0.04	1.80	±0.05	1.98	±0.05	2.52	±0.06
Donadea, IE	342	23.71	±0.48	2.31	±0.06	2.84	±0.06	1.50	±0.03	1.75	±0.05	2.03	±0.05	2.53	±0.06
Enniskillen, IE	389	26.72	±0.65	2.04	±0.05	2.61	±0.05	1.49	±0.03	1.50	±0.04	1.96	±0.04	2.61	±0.06
Breg.Ost.Rav-,D	72	**33.86**	±1.66	2.51	±0.14	2.67	±0.13	1.95	±0.12	1.87	±0.12	2.31	±0.12	**2.97**	±0.13
Farchau, DE	260	23.42	±0.51	2.75	±0.08	**3.00**	±0.08	1.79	±0.05	**1.88**	±0.06	2.40	±0.06	**2.84**	±0.07
Haguenau, FR	287	**35.27**	±0.89	2.95	±0.07	2.52	±0.06	1.95	±0.05	1.65	±0.04	2.38	±0.06	2.45	±0.06
Monterolier, FR	261	29.82	±0.50	2.69	±0.07	2.60	±0.06	1.88	±0.04	1.75	±0.04	2.09	±0.05	2.48	±0.06
Morscwiller, FR	340	30.43	±0.63	2.95	±0.06	2.84	±0.06	2.01	±0.05	1.83	±0.05	2.37	±0.06	2.71	±0.06
Val.Saint.Pier.FR	311	30.61	±0.67	3.03	±0.07	2.68	±0.05	2.01	±0.04	1.68	±0.04	2.43	±0.06	2.52	±0.06
Rabstejn, CZ	219	24.36	±0.59	3.40	±0.09	**3.41**	±0.09	2.36	±0.07	**2.16**	±0.07	3.12	±0.08	**3.25**	±0.08
Szczeciniek, PL	12	24.47	±3.66	2.50	±1.50	**4.50**	±0.50	3.00	±0.00	**2.00**	±0.00	3.60	±0.51	**3.00**	±0.32
Mircze, PL	15	**36.79**	±2.84	3.33	±0.32	2.93	±0.33	1.67	±0.24	1.61	±0.20	2.20	±0.27	2.55	±0.25
Trial means	**6400**	**24.67**	**±0.14**	**3.04**	**±0.02**	**3.29**	**±0.02**	**2.00**	**±0.01**	**2.07**	**±0.01**	**2.60**	**±0.01**	**3.03**	**±0.02**

shown that progenies from northern latitudes and eastern longitudes had the smallest height (Baliuckas *et al.* 1999).

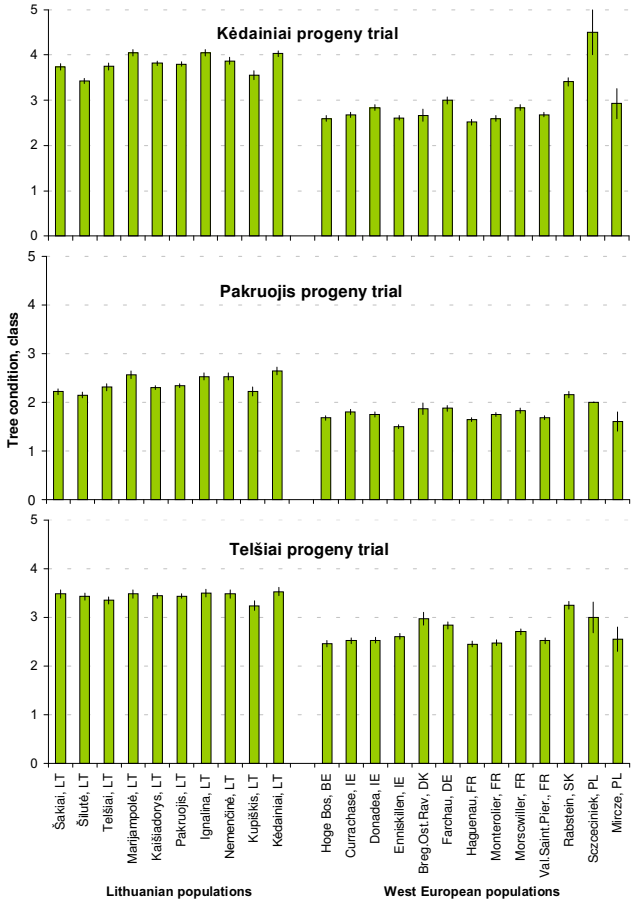

Figure 4. Tree health condition of progenies from Lithuanian and western European populations of *Fraxinus excelsior* in Kėdainiai, Pakruojis, and Telšiai progeny field trials (pins indicate standard errors of populations means)

The genotype and environment interaction (family × field trial) was significant, but comparatively not strong and more or less of the same magnitude as the family variance component (Table 3). Inter-trial (B type) family mean correlations in bud flushing were moderate to strong (0.61-0.71) and highly significant ($P<0.001$). This indicates that specific adaptive reactions are not strongly pronounced at that age. Similar study performed in Sweden with few populations has shown that the family × site interaction might be different in separate populations (Baliuckas *et al.* 1999).

The genotype (at population level) × environment (field trial) interaction was also significant, though not strong (Table 3). That indicates quite even performance of populations' progenies over all experimental sites or, in other words, in different ecological conditions. Three healthiest populations, Marijampolė, Ignalina, and Kėdainiai, were in top positions over all field trials and only their ranking was interchanging. The top ranks of these populations in the Kėdainiai trial, 4th ash provenance region, was respectively 1, 1, and 2, in the Pakruojis trial, 2nd ash provenance region, 2, 3, and 1, respectively, and in the Telšiai trial, 1st ash provenance region, 3, 2, and 1, respectively. The ranking of other populations was less stable, but the Kupiškis and Šilutė populations' progenies were worst by their health condition in all the three trials (Table 5).

Populations differed much in their progeny genetic variation magnitude assessed with the RAPD markers and adaptive traits: the estimates of additive genetic coefficients of variation (CV_A) in bud flushing, one of adaptive traits determining potential for genetic adaptability, within separate populations varied from 6.4 to 29.3% (Table 6). The highest CV_A was obtained for progenies of the Šakiai and Kupiškis populations. Progenies of these populations were also characterized by the highest values of genetic variation parameters of neutral RAPD markers: number and percentage of polymorphic bands, the Shannon index, and the mean genetic distance among individual trees in the population. Different levels of genetic variation in adaptive traits and in neutral RAPD markers indicate differing adaptive potential of populations. Some correspondence between the RAPD markers and adaptive traits genetic variation can be seen. This implies a possibility of at least preliminary evaluation of population adaptive genetic variation with the aid of the RAPD markers. CV_A estimates for adaptive traits of ash were much smaller than the ones for pedunculate oak in a similar experiment and the same age (Baliuckas and Pliura 2003). The same tendency can be observed while comparing with results on mentioned species in Swedish experiment (Baliuckas *et al.* 2000, Baliuckas *et al.* 2001). Such results are very useful indications for possible differences in the gene conservation strategies that could be applied for these tree species.

Additive genetic variation in bud flushing decreased very much in majority of populations in the Pakruojis field trial due to severe progeny spring frost damage (Table 6). Analogous to these results, when stressors influenced genetic variation by diminishing it, were obtained in the phytotron experiment where Lithuanian ash populations were exposed to large ozone doses: CV_A for seedling height was 47.7-49.4% in the control treatment and decreased to 10.7-30.8% in the O_3 treatment with 240 µg /m^3 dosage (Pliūra *et al.* 2006).

Population differences in adaptive traits (mean estimates of populations) and in additive genetic variances within each population are very important criteria indicating target populations for gene conservation.

Table 5. Tree height, bud flushing phenology and tree health condition of western European and Lithuanian populations of *Fraxinus excelsior* in three progeny field trials

Populations, country	Number of trees in trial	Nursery trial		Kėdainiai field trial				Pakruojis field trial				Telšiai field trial			
		Tree height, cm		Phenology, class		Condition, class		Phenology, class		Condition, class		Phenology, class		Condition, class	
		Mean	±std.er.	Mean.	±std.er.	Mean	±std.er.	Mean	±std.er.	Mean	±std.er.	Mean	±std.er.	Mean	±std.er.
Lithuanian:															
Šakiai, LT	236	**23.34**	±0.70	3.36	±0.08	3.74	±0.07	2.31	±0.06	2.22	±0.06	2.99	±0.07	3.48	±0.08
Šilutė, LT	297	**33.48**	±1.01	3.15	±0.07	3.43	±0.06	2.12	±0.05	2.15	±0.06	3.09	±0.07	3.43	±0.07
Telšiai, LT	268	**20.54**	±0.51	3.47	±0.08	3.75	±0.08	2.26	±0.06	2.31	±0.07	2.99	±0.08	3.35	±0.07
Marijampolė, LT	229	16.78	±0.55	3.69	±0.07	**4.05**	±0.07	2.30	±0.06	**2.56**	±0.08	2.96	±0.08	**3.48**	±0.08
Kaišiadorys, LT	612	20.03	±0.36	3.65	±0.05	3.82	±0.05	2.23	±0.04	2.30	±0.04	3.12	±0.05	3.45	±0.05
Pakruojis, LT	681	19.08	±0.37	3.16	±0.05	3.80	±0.05	2.05	±0.03	2.34	±0.04	2.88	±0.05	3.44	±0.05
Ignalina, LT	249	17.89	±0.51	3.65	±0.07	**4.05**	±0.07	2.39	±0.06	**2.53**	±0.07	2.97	±0.08	**3.50**	±0.08
Nemenčinė, LT	205	16.21	±0.49	3.60	±0.08	3.87	±0.08	2.33	±0.06	2.53	±0.07	2.99	±0.08	3.48	±0.08
Kupiškis, LT	192	16.71	±0.48	3.20	±0.09	3.56	±0.10	1.89	±0.07	2.22	±0.09	2.73	±0.09	3.24	±0.10
Kėdainiai, LT	225	16.61	±0.48	3.31	±0.08	**4.03**	±0.07	2.06	±0.06	**2.64**	±0.08	2.83	±0.07	**3.53**	±0.08
West European:															
Hoge Bos, BE	267	30.69	±0.68	2.62	±0.07	2.60	±0.06	1.74	±0.04	1.68	±0.05	1.95	±0.05	2.46	±0.06
Currachase, IE	300	27.00	±0.57	2.12	±0.05	2.68	±0.06	1.56	±0.04	1.80	±0.05	1.98	±0.05	2.52	±0.06
Donadea, IE	342	23.71	±0.48	2.31	±0.06	2.84	±0.06	1.50	±0.03	1.75	±0.05	2.03	±0.05	2.53	±0.06
Enniskillen, IE	389	26.72	±0.65	2.04	±0.05	2.61	±0.05	1.49	±0.03	1.50	±0.04	1.96	±0.04	2.61	±0.06
Breg.Ost.Rav-,D	72	**33.86**	±1.66	2.51	±0.14	2.67	±0.13	1.95	±0.12	1.87	±0.12	2.31	±0.12	**2.97**	±0.13
Farchau, DE	260	23.42	±0.51	2.75	±0.08	**3.00**	±0.08	1.79	±0.05	**1.88**	±0.06	2.40	±0.06	**2.84**	±0.07
Haguenau, FR	287	**35.27**	±0.89	2.95	±0.07	2.52	±0.06	1.95	±0.05	1.65	±0.04	2.38	±0.06	2.45	±0.06
Monterolier, FR	261	29.82	±0.50	2.69	±0.07	2.60	±0.06	1.88	±0.04	1.75	±0.04	2.09	±0.05	2.48	±0.06
Morscwiller, FR	340	30.43	±0.63	2.95	±0.06	2.84	±0.06	2.01	±0.05	1.83	±0.05	2.37	±0.06	2.71	±0.06
Val.Saint.Pier.FI	311	30.61	±0.67	3.03	±0.07	2.68	±0.05	2.01	±0.04	1.68	±0.04	2.43	±0.06	2.52	±0.06
Rabstejn, CZ	219	24.36	±0.59	3.40	±0.09	**3.41**	±0.09	2.36	±0.07	**2.16**	±0.07	3.12	±0.08	**3.25**	±0.08
Sczceciniek, PL	12	24.47	±3.66	2.50	±1.50	**4.50**	±0.50	3.00	±0.00	**2.00**	±0.00	3.60	±0.51	**3.00**	±0.32
Mircze, PL	15	**36.79**	±2.84	3.33	±0.32	2.93	±0.33	1.67	±0.24	1.61	±0.20	2.20	±0.27	2.55	±0.25
Trial means	**6400**	**24.67**	**±0.14**	**3.04**	**±0.02**	**3.29**	**±0.02**	**2.00**	**±0.01**	**2.07**	**±0.01**	**2.60**	**±0.01**	**3.03**	**±0.02**

Table 6. Family variance components as percent of the total random variation, its standard errors, heritability, and genetic coefficient of additive variation (CV_A) in each western European and Lithuanian population of *Fraxinus excelsior* in each progeny field trial for bud flushing phenology and data on diversity of DNA RAPD markers. The highest CV_A and marker diversity characteristics indicated in bold

Population	Kėdainiai field trial				Pakruojis field trial				Telšiai field trial				DNA markers (RAPD)*				
	Number of seedlings	Family variance component ±std. err., %	Heritability ±std. error	CV_A, %	Number of seedlings	Family variance component ±std. err., %	Heritability ±std. error	CV_A, %	Number of seedlings	Family variance component ±std. err., %.	Heritability ±std. error	CV_A, %	Polymorphic DNA bands		Shannon index	Mean genetic distance
													Number	Percentage		
Lithuanian:																
Šakiai, LT	46	9.7 ±6.4	0.39 ±0.23	**21.2**	50	3.4 ±3.2	0.13 ±0.12	**14.3**	49	10.6 ±6.6	0.42 ±0.23	**25.6**	**68**	**90**	**0.52**	0.24
Šilutė, LT	24	4.8 ±4.1	0.19 ±0.14	15.8	50	1.3 ±2.4	0.05 ±0.09	9.2	24	7.0 ±5.2	0.28 ±0.18	**20.1**	**70**	**92**	**0.53**	0.25
Telšiai, LT	49	12.7 ±7.5	0.51 ±0.26	**24.8**	49	0.3 ±2.1	0.01 ±0.07	4.5	50	3.9 ±3.6	0.16 ±0.13	16.1	**70**	**92**	**0.53**	**0.31**
Marijampolė, LT	48	3.7 ±4.0	0.15 ±0.14	11.7	52	6.9 ±5.2	0.28 ±0.18	**21.5**	50	3.6 ±3.6	0.14 ±0.13	15.1	63	83	0.46	0.26
Kaišiadorys, LT	125	5.0 ±2.7	0.20 ±0.10	14.0	134	3.8 ±2.3	0.15 ±0.08	17.0	133	5.9 ±2.8	0.23 ±0.10	17.8	53	70	0.38	0.22
Pakruojis, LT	135	9.9 ±3.7	0.40 ±0.13	**23.2**	141	8.4 ±3.3	0.34 ±0.12	**24.0**	141	1.9 ±1.6	0.08 ±0.06	10.9	44	58	0.31	0.18
Ignalina, LT	49	6.3 ±4.9	0.25 ±0.17	14.9	50	1.8 ±2.8	0.07 ±0.10	10.8	50	0.6 ±2.1	0.02 ±0.08	6.4	54	71	0.40	0.21
Nemenčinė, LT	48	7.6 ±5.8	0.30 ±0.21	17.2	49	1.7 ±2.8	0.07 ±0.10	10.1	49	1.5 ±2.6	0.06 ±0.10	9.5	50	66	0.36	0.19
Kupiškis, LT	44	4.1 ±5.9	0.16 ±0.16	**15.8**	39	3.6 ±4.3	0.14 ±0.16	**18.0**	39	7.9 ±6.7	0.32 ±0.23	**23.7**	**65**	**86**	**0.50**	**0.29**
Kėdainiai, LT	49	8.4 ±5.8	0.34 ±0.20	20.3	47	1.0 ±2.6	0.04 ±0.10	9.1	47	7.3 ±5.8	0.29 ±0.20	**20.3**	59	78	0.41	**0.27**
West European:																
Hoge Bos, BE	60	0.7 ±2.2	0.03 ±0.09	7.1	61	0	0 .	0	61	0	0	0				
Currachase, IE	80	7.3 ±4.6	0.29 ±0.16	21.7	86	3.4 ±3.4	0.13 ±0.12	14.5	86	1.1 ±2.5	0.04 ±0.09	9.0				
Donadea, IE	85	6.2 ±3.8	0.25 ±0.14	21.4	94	4.7 ±3.4	0.19 ±0.13	17.8	93	9.2 ±4.6	0.37 ±0.17	**26.7**				
Enniskillen, IE	87	2.4 ±2.4	0.10 ±0.09	13.3	83	3.1 ±3.0	0.12 ±0.11	15.3	85	4.9 ±3.3	0.20 ±0.12	18.9				
Breg.Ost.Rav,D	15	0 .	0 .	0	15	0	0 .	0	15	7.2 ±11.6	0.29 ±0.37	**21.5**				
Farchau, DE	54	11.9 ±7.5	0.47 ±0.23	**29.3**	57	3.6 ±4.2	0.14 ±0.13	15.7	61	3.6 ±3.1	0.14 ±0.12	17.0				
Haguenau, Fr	78	1.6 ±2.9	0.07 ±0.10	10.0	81	1.3 ±2.9	0.05 ±0.10	9.8	83	3.4 ±3.3	0.14 ±0.12	15.7				
Monterolier, FR	83	2.2 ±3.3	0.09 ±0.12	12.2	86	5.9 ±3.7	0.24 ±0.14	**19.6**	84	0 .	0 .	0				
Morscwiller, FR	80	8.7 ±4.6	0.35 ±0.17	**21.8**	84	2.8 ±2.9	0.11 ±0.11	13.8	86	3.6 ±3.2	0.14 ±0.11	17.5				
Val.Saint.Pier.FR	79	10.9 ±5.5	0.44 ±0.19	**23.7**	83	3.4 ±3.4	0.14 ±0.12	14.1	82	2.5 ±2.6	0.10 ±0.10	12.7				
Rabstejn, CZ	55	5.7 ±5.0	0.23 ±0.17	17.6	56	8.1 ±6.2	0.32 ±0.21	**22.9**	50	13.1 ±7.2	0.52 ±0.25	**27.5**				

* - Data from Žvingila *et al.* 2005

These parameters are also used when constructing gene conservation strategy and program. Genetic variation estimates for adaptive traits in the Ignalina and Nemenčinė populations were small in many cases. So, these populations would be considered as problematic ones in aspects of broad genetic adaptability and sustainability, but there is a possibility that these populations posses some specific adaptedness. Nevertheless, large genetic variation in phenologic traits of the Kupiškis population progeny was followed by the worst tree health condition assessments in all three field trials. Such contradictory data call for need of additional investigation of adaptive traits in the nearest future and also for repetition of assessments over few years in order to make more precise classification of populations by their potential for gene conservation.

Conclusions

The population effect for all adaptive traits, bud flushing phenology, height, and tree health condition, in progenies from Lithuanian and western European populations of *Fraxinus excelsior* studied in three progeny field trials was strongly significant ($P<0.001$), thus revealing pronounced adaptively significant population structure.

Progenies of the Lithuanian populations had earlier bud flushing and better health condition than progenies of the western European populations in all three trials, but tree height was smaller (except the Šilutė population).

The additive coefficient of genetic variation of bud flushing phenology and tree health condition of progenies ranged totally from 30.3 to 40.8%, indicating high genetic diversity of the material collected in progeny field trials and, thus, good potential for gene conservation *ex situ* and for tree breeding of *Fraxinus excelsior* in Lithuania.

The estimates of additive genetic coefficients of variation (CV_A) in bud flushing, one of key adaptive traits determining potential for genetic adaptability, within individual populations varied from 6.4 to 29.3%. The Šakiai and Kupiškis populations had high genetic variation of both adaptive traits and RAPD markers, while other populations had differing levels of RAPD and adaptive traits genetic variation, thus indicating differing adaptive potential of individual populations.

The correlation between bud flushing and tree condition of populations was positive and strong, $r = 0.81$, 0.78, and 0.92 in the Kėdainiai, Pakruojis, and Telšiai field trials, respectively, indicating that that earlier flushing populations have better tree health condition.

The genotype × environment interaction at population × experimental trial level was significant, though not strong, thus indicating quite even performance of populations' progenies over all experimental sites. The family × trial interaction was significant, but comparatively not strong, of the same magnitude as the family variance component.

The genetic changes within population variation across sites were population specific. Such changes can alter adaptation, sustainability, and competitive ability of newly formed populations in a hardly predictive way.

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ГЕНЕТИЧЕСКАЯ ВАРИАЦИЯ ПОТОМСТВА ЛИТОВСКИХ И ЗАПАДНО ЕВРОПЕЙСКИХ ПОПУЛЯЦИЙ *FRAXINUS EXCELSIOR* L.

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Резюме

Исследования проводились с целью изучения генетической вариации адаптивных признаков и ДНК маркеров у полусибсового потомства Литовских и Западно Европейских популяций в экспериментальных насаждениях *Fraxinus excelsior*, расположенных в трёх разных лесосеменных районах Литвы. Потомство Литовских популяций было более раннее по распусканию листьев во всех трёх насаждениях и менее подвержено болезням, чем потомство Западно Европейских популяций, но уступало им по высоте (кроме популяции Шилуте). Полученные популяционные и семейные генетические эффекты были достоверны для всех изучаемых признаков. Несмотря на то, что семейный компонент дисперсии не был высок и варьировал в рамках 11.6 и 22.6%, генетический коэффициент аддитивной дисперсии был значительный и в некоторых насаждениях варьировал от 30.3 до 36.8%. Были получены достаточно различные значения генетической вариации адаптивных признаков и RAPD маркеров у исследуемых популяций, и это указывает на их разный потенциал к адаптации. Высокие показатели генетической вариации адаптивных признаков и RAPD маркеров были установлены у популяций Шакяй и Купишкис, тогда как в остальных популяциях эти показатели различались между собой. Изменения генетической внутрипопуляционной вариации адаптивных признаков в разных экспериментальных насаждениях у некоторых популяций не соответствовали общей тенденции. Такие различия могут трудно предсказуемо менять адаптацию, стабильность и конкурентоспособность новых формирующихся популяций.

Ключевые слова: *Fraxinus excelsior*, популяции, потомство, полусибсовые семьи, генетическая вариация, адаптивные признаки, взаимодействие генотипа и среды.