Genetic Variation in Adaptive Traits and Ecological Sensitivity of Black Alder

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Fifty eight to 85 half sib progenies of black alder (*Alnus glutinosa* L.) from 17 Lithuanian populations were studied for 5 years in 3 test plantations which were established in different forest eco-regions of Lithuania. Objectives of the study were: (1) to assess the amount of within- and among-population variation of traits of adaptive significance (e.g., juvenile height growth, phenology and frost resistance); (2) to evaluate how genetic variation is affected by different ecological conditions; and (3) to evaluate stability and reaction norms of families and populations across environments.

Strongly significant effects of site conditions were found for most growth traits, indicating a high phenotypic plasticity of black alder and indicating the ability of the species for short-term response to changes in climate and environment. All over the 3 test plantations the family variance component was relatively low, varying from 2.1 to 3.1%. However, in every test plantation the family effect was often significant and variance component reached up to 38.3%. The heritabilities and coefficient of additive variation for growth and phenology traits studied were generally larger than for other traits, but these also varied from site to site. A sufficient amount of additive variance within populations and among population variance suggests that black alder has potential for adaptation via natural selection during the juvenile stage if environmental conditions change. The variance component of genotype x environment interactions in variation of different traits indicating differences among families in their plastic response was slightly larger than their family variance component. The absence of significant genetic correlation for some traits among trials also indicated that $g \times e$ interaction plays a significant role in variation. However, in general the performance of the families across environments was rather stable: only 16.5% of the families contributed significantly to the $g \times e$ interaction for phenology and 24.7% for height growth, and their ecovalence estimates were generally low (<5.5%). Each family combined different levels of stability, plasticity, type of plastic response, type of adaptation, and level of specialization. These differences in plasticity and adaptability in some cases should be considered in order to maximise the genetic gain in forest tree breeding. The largest differences between families in response to the range of environments were within the most productive populations (Plungė (36) and Marijampolė (33)). The significant genetic correlation found between height growth and frost resistance within individual progeny trials indicated that frost negatively influenced the growth. Over all 3 trials the significant population effect was found for bud flushing only. The population variance component was up to 8.4%, although in each trial the population variance was higher (from 13.8% to 39.8%). This variation among families and among populations facilitates developing efficient Multiple-Population (MPBS) joint breeding and gene conservation system of black alder.

Keywords: *Alnus glutinosa*, populations, families, genetic variation, heritability, genetic correlations, phenotypic plasticity, reaction norms, adaptation.

Introduction

Black alder (*Alnus glutinosa* L.) is becoming an important forest tree species due to its multiple uses both in the forestry and industry. Stands of black alder with long rotations can produce logs and wood of very good quality for the wood and furniture industries, but in short-rotation, special-purpose plantations the species is suitable for biomass production (Krstinić 1994). Black alder is a fast-growing species that has the ability to fix atmospheric nitrogen due to a symbiotic actinomycete, *Frankia alni* (Wheeler and Lawrie 1976). Black alder has a wide range of natural distribution, and natural populations of the species are found in different ecological conditions that promote climatic or edaphic differentiation. Such a wide range of distribution combined with relatively small and isolated populations causes a high degree of variability (Weisgerber 1974). The results of provenance research revealed very distinct genetic differences in survival, production, trunk shape, and root system features for the species (Münk 1936; Schmit-Vogt 1971; Mejnarto-

wicz, 1972; Liepe, 1990; Krstinić et al. 1992; Baliuckas et al., 1999). Significant differences between black alder provenances have been found in phenological characteristics, such as budburst and vegetation time, suggesting genetic differences between provenances (Rubcov 1968, Bialobok et al. 1980, Baliuckas et al. 1999). Some degree of geographical population structuring within species of *Alnus glutinosa* and *A. cordata* in DNA was found in Italy also in chloroplast DNA studies using PCR-RFLP method and nuclear genome studies by ISSR analysis (King and Ferris 2000). However within population variation of DNA markers was much higher (43.65% against 6.15%).

It is commonly assumed that forest trees are adapted to local environmental conditions. However, genetic variation between populations in phenology and other adaptive traits is counteracted by high gene flow expected in forest tree species, high plasticity, and significant climate variation during the year and during whole ontogenesis. Forest tree species have been exposed to significant changes in environmental conditions during the last ten thousand years and have responded by migration and/or adaptation to the most suitable habitats (Huntley and Birkes 1983). Populations of forest tree species still grow in very heterogeneous environments - in different eco-climatic conditions, forest communities, habitats, and sites. Due to the warming of the global climate, more extreme temperatures and levels of precipitation are predicted to occur (Kattenberg et al. 1996), therefore increasing the environmental stress on trees in the coming decades. Moreover, increased temperature and humidity are expected to favour the epidemic spread of pathogens and parasites. The ability of forest tree species to adapt to the direct and indirect consequences of quick global climate warming is difficult to predict.

There are two strategies of plant adaptation that can be identified: genetic variation and phenotypic plasticity. In a population that has considerable genetic variation, as the environment changes the population adapts when the best genotypes survive and reproduce, but maladapted genotypes disappear due to natural selection. Natural selection results in formation differences in allele- and genotype frequencies between populations (Hartl 1988). When rapid adaptation is required or when genetic variation is lacking, plants respond to temporal or spatial fluctuations by modifying their phenotype (Schmalhausen 1949). This specific response to a certain range of conditions for a particular character or set of traits is called *phenotypic plasticity* (Bradshaw 1965). Studies of plastic response along an environmental gradient (e.g., Knight 1970, Roberds et al. 1976, Gupta and Lewontin 1982, Gregorius and Namkoong 1986, Namkoong et al. 1992) indicate that reaction norms and responses to environment gradients vary significantly among genotypes.

One hypothesis suggests that genetic variation and plasticity represent alternative strategies for coping with environment heterogeneity (Marshall and Jain 1968, Jain 1979). Other hypotheses consider that genetic variation and phenotypic plasticity are positively correlated (Gillespie and Turell 1989, Goldstein and Holsinger 1992). Moreover, phenotypic plasticity is considered to be a trait in itself that is under genetic control (Bradshaw 1965, Schlichting 1986, Scheiner 1993) and can evolve independently of the trait (Schlichting and Levin 1984). A phenotypic response can be adaptive when enhancing fitness in a changing environment (Sultan and Bazzaz 1993), or non-adaptive when resulting in deterioration of individual fitness expressed in reduced growth, which reflects the inevitable metabolic or developmental response (Sultan 1987, 1995). High adaptation in heterogeneous environments can be achieved by both phenotypic plasticity and stability. In the first case, populations may be subjected to local selection resulting in specialized genotypes that perform better in local (optimal) environments than in non-local environments (Taylor and Aarssen 1988). The phenotypic plasticity of such genotypes is high. The second case refers to situations when selection favours genotypes capable of buffering their phenotypes in changing environments. The phenotypic plasticity of such genotypes is low.

Analysis of variance of data from testing progenies in different environments gives a possibility of evaluating genetic variation, phenotypic plasticity, and genetic variation of phenotypic plasticity. The variance due to the site environment quantifies the phenotypic plasticity. Genetic variation of phenotypic plasticity can be quantified by genotype x environment interaction variance in ANOVA, or by genetic correlation between the genotypic means across environments (Falconer and Mackay 1996, Schlichting and Levin 1984). These analyses allow for the evaluation of general patterns of plastic response in the whole experiment. Many methods and caharacteristics can be used to evaluate the extent and character of plasticity for an individual family or population. These methods include: (a) range of variation family means (or breeding values) across environments; (b) sum of squares of deviations or standard deviation of family means across environments; (c) coefficient of variation of family means across environments; (d) Wricke ecovalence coefficients; (e) Shukla stability variance; (f) correlation coefficients between family means across the environment; (g) evaluation of reaction norms using the Finlay-Wilkinson (1963) parameters of linear regression equation (intercepts and slope coefficients); (h) Eberhardt-Russell stability parameter as residual variance of linear regression (Eber-

hardt-Russell 1966); (i) evaluation of reaction norms using parameters of polynomial (Knight 1973) or exponential (Gregorius and Namkoong 1986, Namkoong et al. 1992) functions and others.

The objectives of the study were: (1) to assess the amount of within- and among-population variation in traits of adaptive significance (e.g., juvenile height growth, phenology and frost resistance) of black alder open-pollinated progenies; (2) to evaluate how genetic variation is affected by different ecological conditions within- and among progeny trials; and (3) to evaluate phenotypic plasticity, stability, and reaction norms of families and populations across environments.

Material and methods

Material

Seeds were collected from 5-6 trees in each of 17 populations of Lithuanian black alder (*Alnus glutinosa* L.). In 1998, three progeny test plantations were established in 3 forest ecoclimatic regions of Lithuania on different sites using seedlings from all 17 populations. In each locality, all 17 populations were represented by 5-6 half-sib families in 5 randomised blocks, 10 tree-plot per family in each block. The spacing was 2.0 m between rows and 1.5 m between trees in each row. The characteristics of the test plantations and number of families tested are presented in Table 1.

Table 1. Characteristics of *Alnus glutinosa* progeny test plantations of the 1998 series.

Nr	Location of test plantation	Area, ha	Latitude	Longitude	Altitude a.s.l., m	Forest eco-region	Climate type/continentality index	Site index	Number of populations /families
1	Kaunas forest enterprise	1.2	55°06'	23°53'	70	5	Transitional/29	Nc	17/74
2	Šiauliai forest enterprise	1.6	55°58'	23°09'	120	2	Transitional/27	Nd	17/85
3	Šilutė forest enterprise	1.5	55°13'	21°33'	12	4	maritime / 25	Ld	17/58

Assessments

When the trees were 3 and 5 years of age the following characteristics that reflect adaptedness were measured and analysed: survival, height of tree, stem diameter, stage of flushing, frost resistance, and resistance to fungi diseases. The bud flushing stage was rated 1 to 5 (1 - dormant bud; 2 - bud is swollen; 3 - bud is opened, leaves emerging; 4 - elongation of the apical shoot started, spread of the leaves started; 5 - elongation of lateral shoots started, leaves are spread), frost resistance was rated 1 to 4 (1 - stem and shoots dead; 2 - shoots dead; 3 - shoots and buds injured; 4 - no visible injury), resistance to fungi diseases was rated 0 to 1 (0 - dead from fungi; 1 - not damaged).

Statistical analysis

In the analysis of variance of growth traits, in order to reduce the influence of significant differences in frost damages on individual, family, and population levels and suppression of growth on patterns of variation, trees that were shorter in height than the family mean by 2σ were removed. No covariates were used in the analysis of variance.

Variance analysis was done using the MIXED procedure in the SAS Software (SAS Institute Inc. SAS/STAT® software.). Mixed model equations (MME) and the restricted maximum likelihood (REML) method were used for computing variance components.

The following linear models were used for joint analyses of the 3 progeny trials together and for separate analyses of individual treatments

1) Joint:

$$y_{ijlmn}=\mu+b_i(t)+t_j+f_l(p)_m+p_m+ft_{lj}+pt_{mj}+\varepsilon_{ijlmn}$$

2) Separate:

$$y_{ilmn}=\mu+b_i+f_l(p)_m+p_m+\varepsilon_{ilmn}$$

where y_{ijlmn} and y_{ilmn} are values of a single observation, μ is the grand mean, a is a constant, t_j is the fixed effect of trial j, $b_i(t)_j$ is the fixed effect of block i within trial j, b_i is the fixed effect of block i, $f_l(p)_m$ is the random effect of family l within population m, p_m is the random effect of population m, ft_{lj} is the random effect of interaction between family l and trial j, pt_{mj} is the fixed effect of interaction between population m and trial j, ε_{ijlmn} and ε_{ilmn} are random error terms.

Genetic parameter estimates

Genetic parameters were derived from the model 2 separately for each trial (progeny test plantation). The families that were considered as half-sibs and genetic parameters were interpreted as:

Additive genetic variance: $\sigma_A^2=4\sigma_f^2$

Environmental variance: $\sigma_E^2=\sigma_e^2-3\sigma_f^2$

Additive genetic coefficients of variation:

$$CV_A=\frac{\sqrt{4\cdot\sigma_f^2}}{\overline{X}}\cdot 100$$

Individual tree heritabilities: $h_i^2=\frac{\sigma_A^2}{\sigma_A^2+\sigma_E^2}$

Genetic correlations: $r_A=\frac{\sigma_{A_1A_2}}{\sqrt{\sigma_{A_1}^2\times\sigma_{A_2}^2}}$

where σ_f^2 is the family variance component of population, σ_e^2 is the error variance component, $\overline{X}$ is the phenotypic mean of the trait, $\sigma_{A_1A_2}$ is the covariance between traits 1 and 2, $\sigma_{A_1}^2$ and $\sigma_{A_2}^2$ are the additive genetic variance of traits 1 and 2, respectively.

Standard errors of individual heritabilities were calculated as described for unbalanced designs by-

Becker (1984). Two types of genetic correlations were calculated: between different traits within an individual trial (Type A) and between the same trait assessed in different trials (Type B; Burdon 1977). Type B genetic correlations were calculated to evaluate the contribution of each pair of trial to total *genotype x environment* interaction. Genetic correlation coefficients were calculated using the outcomes (breeding values) from the 'solution' option of the MIXED procedure, SAS Software.

Stability analysis of families

Stability of families was estimated across three trials. The preliminary extent of phenotypic plasticity for each family was estimated calculating: (a) a range of variation of breeding values; (b) coefficient of variation; and (c) sum of squares of deviations of breeding means (breeding value + trial mean) across environments. Breeding values were calculated for individual families within each trial using the BLUP method, option 'solutions' to the mixed linear model of variance analysis, procedure MIXED of the SAS software.

To estimate the contribution of each family to the family x trial interaction variances, the ecovalence values of families by populations were calculated on family means across trials using a standard method (Wricke, 1962). Alternative ecovalence estimates were calculated on the individual observation level, by using breeding values obtained from the MIXED procedure of the SAS. The ecovalence value as a measure of interaction variance for each family was expressed in percent of the total interaction variance. This type of analysis was condicted for traits where family x trial interaction was significant. The Shukla's stability variances were computed and the significance of the ecovalences was tested using the method developed by Shukla (1972). In calculating ecovalences to better fulfill the assumptions behind the linear model and thus reduce the scale effects of different blocks or trials in joint analysis, the data were transformed to equal additive genetic variance by using the method of Dancll (1988). The method is described further by Ericsson (1994). For each trait and trial, the assessed values for each tree were multiplied by a scaling factor which for the *i*th trial was $k_i = \sigma_{\bar{A}} / \sigma_{A_i}$, where $\sigma_{\bar{A}}$ is the mean additive genetic standard deviation over all 3 trials, and σ_{A_i} is the additive genetic standard deviation for the *i*th trial.

The evaluation of reaction norms of individual families was done using Finlay-Wilkinson (1963) parameters, intercepts and slope coefficients of linear regression of family means against mean performance over environments. In addition the Eberhardt-Russell stability parameter, residual variance of linear regression was calculated (Eberhardt-Russell 1966).

Stability analysis of populations

Similar to height growth stability analysis of families across trials, the preliminary evaluation the stability of populations was performed by estimating: (1) a range of variation of population breeding values; (2) coefficient of variation; and (3) sum of squares of deviations of population breeding means (breeding value + trial mean) across environments. Breeding values for individual populations within each trial were calculated using option 'solutions' to the mixed linear model of variance analysis, procedure MIXED of the SAS software. Individual observations were used in analysis of variance. The population effect was considered random.

To estimate the contribution of each population to the population x trial interaction variances, the ecovalence values of populations were computed, using the breeding values calculated from the MIXED procedure for individual populations within each treatment. To reduce the scale effects of different trials in joint analysis, the data were transformed to equal population genetic variance using the method described above. For each trait and trial, the assessed values for each seedling were multiplied by a scaling factor which for the *i*th trial was $k_i = \sigma_p / \sigma_{p_i}$, where σ_p is the mean population standard deviation over all 3 trials and σ_{p_i} is the population standard deviation for the *i*th trial.

Similar to the evaluation of reaction norms of families, Finlay-Wilkinson (1963) parameters, intercepts and slope coefficients of linear regression of family means against mean performance across environments and Eberhardt-Russell stability parameter (1966), residual variance of linear regression, were calculated for individual populations as well.

Results

Among environment variation

As presented in Table 2, there were strongly significant trial and block effects for most growth, phenology, and resistance traits, except trial effect for height growth and block effect for resistance to fungi diseases.

Within population variation and family × environment interactions

Throughout the 3 test plantations, the family variance component was relatively low, varying from 2.1 to 3.1% (Table 2). Family effect was significant only for frost resistance. The family effect in every single test plantation were often significant for most of traits, with high variance components reaching up to 38.3% (Table 3). As presented in Table 3, the heritabilities

and CV_A for growth and phenology traits were generally larger than for other traits, however they varied from site to site.

Table 2. Variance components for random effects as a percent of the total random variation, and significance of fixed effects σ_f^2, σ_p^2, σ_{fl}^2, and σ_{pt}^2 are the variance components for family, population, family x trial and population x trial interactions, respectively. Level of significance is denoted by: *- 0.05>P>0.01, ** - 0.01> P>0.001, *** - P<0.001. Results are from a joint mixed linear model (1) analysis of variance of data from *Alnus glutinosa* progeny growth in 3 trials

Trait	Variance components of random effects, %				Significance of fixed effects	
	σ_f^2	σ_p^2	σ_{fl}^2	σ_{pt}^2	block	trial
Height (H)	2.1	0	9.7***	0	***	
Stem diameter (D)	3.1	0.0	4.3	0	***	***
Bud flushing stage (BF)	0	8.4*	5.6***	8.3***	***	*
Frost resistance (FR)	2.1*	0.6	4.8***	0.5	***	***
Resistance to fungi diseases (RES)	0	0	1.0**	0.4		**

Table 3. Mean values, family components, standard errors, individual habitabilities, and additive genetic coefficients of variation of different traits of *Alnus glutinosa* open-pollinated families for 3 trials. Results are from a mixed linear model (2) analysis of variance of data in separate trials.

Trait	Trial	Mean	Family variance component,		Family additive	
			%	±se	h_i^2	CV_A (%)
Height (H, cm)	Kaunas	90.91	10.8	±2.9	0.43	19.5
	Šiauliai	96.53	13.2	±2.8	0.53	22.0
	Šilutė	104.21	17.6	±8.3	0.70	20.6
Stem diameter (D, mm)	Kaunas	20.20	7.0	±2.2	0.28	14.1
	Šiauliai					
	Šilutė	21.39	12.7	±7.0	0.51	17.3
Bud flushing stage, (BF, class)	Kaunas	3.42	7.4	±2.4	0.30	20.8
	Šiauliai	3.37	17.9	±3.5	0.72	24.5
	Šilutė	3.45	38.3	±11.4	1.53	45.3
Frost resistance (FR, class)	Kaunas	3.14	9.2	±2.6	0.37	7.5
	Šiauliai	3.13	10.3	±2.3	0.41	9.1
	Šilutė	3.05	0.9	±4.8	0.04	1.5
Resistance to fungi diseases (RES, class)	Kaunas	0.93	5.2	±2.0	0.21	12.6
	Šiauliai	0.90	2.3	±1.1	0.09	10.1
	Šilutė	0.91	0		0	0

The variance component of genotype (at the family level) x environment interaction in variation of different traits, which characterise the differences in type of phenotypic plasticity, was rather small. However, it was significant and 1.4 or more times larger than the family variance component (Table 3). Fourteen families (16.5% of the total number of families tested) contributed significantly to the *g x e* interaction for phenology and 21 families (24.7%) for height growth with generally low estimates of the ecovalence values (<5.5%) (Figs. 1 and 2, Table 5). The highest Wricke's ecovalences and Shukla stability variances (Tables 4 and 5) indicated that families 66, 134, 104, and 120 contributed most to the total *g x e* interaction in height growth. Low stability of these families (Table 4) was also indicated by the largest variation of breeding values, largest coefficient of variation and sum of squares of deviations of breeding values across environments. The highest regression coefficients (Finlay-Wilkinson parameter, Table 5) were in families 66, 103, 104, and 120. Only families 120 and 103 had high Eberhardt-Russell stability parameter, residual variance of linear regression. For the phenology trait of the bud-flushing stage, the most unstable families were 74, 95, 64 and 70, which had the highest Wricke's ecovalences, Shukla stability variances, and other characteristics (Fig. 2). These families contributed most to the *g x e* interaction. The absence of significant genetic correlation among trials except bud flushing in the Kaunas and Šiauliai trials with the Šilutė trial (Table 6) indicates that the *g x e* interaction plays a significant role in the variation of most traits. Within individual progeny trials significant genetic correlation was found between height growth and frost resistance (Table 6), the highest families were less damaged. However, no significant genetic correlation was found between bud flushing stage and height growth or frost resistance.

Among population variation and population × environment interactions

Over the entire experiment the significant variance component of the population effect was found only for bud flushing, reaching up to 8.4%. It is noteworthy that the population variance component was present in the absence of the family variance component. In each single trial the population variance component was higher than throughout the 3 test plantations and comprised 13.8% in the Šiauliai trial and 39.8% in the Šilutė trial. However, it was insignificant in the Kaunas trial. The Kazlų Rūda (52) and Šakiai (34) populations were flushing earliest, while the Kuršių Nerija (35) and Šiauliai (20) populations were among the last to flush (Fig. 2). These populations kept the same phenology behaviour over different test plantations. However, many populations changed their rank across the 3 test plantations.

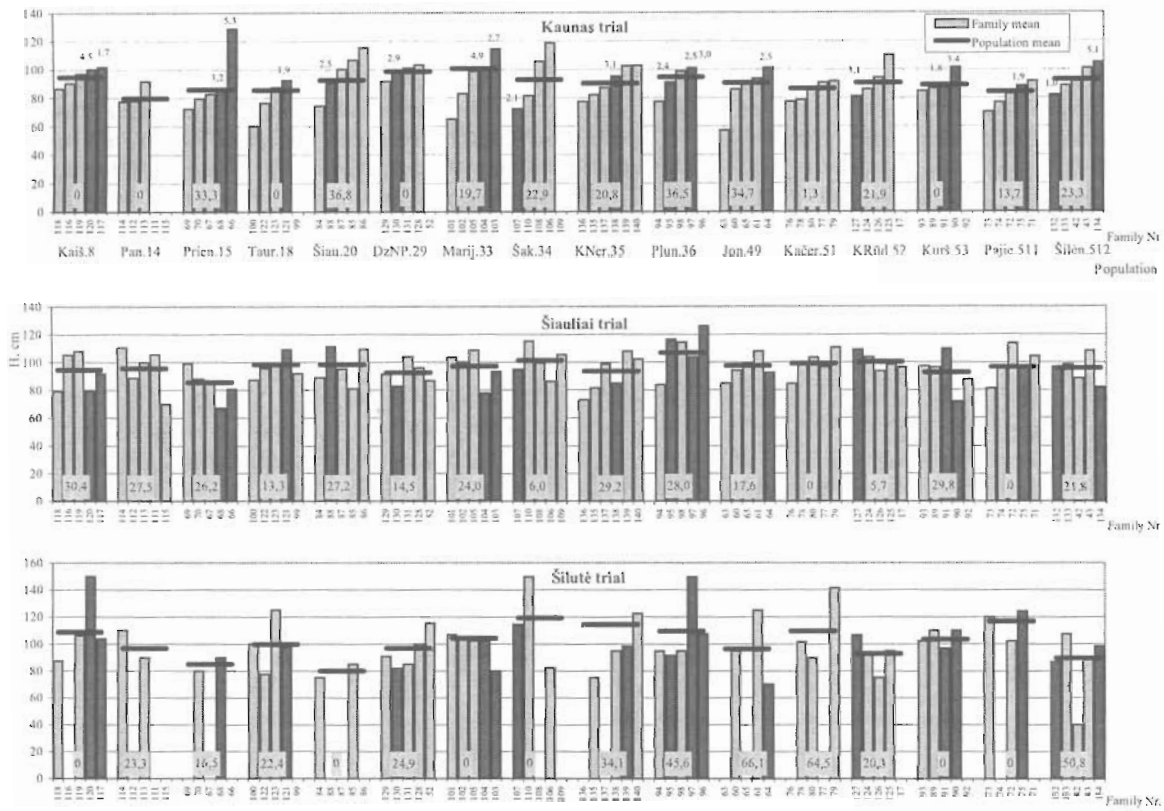

Figure 1. Height growth of *Alnus glutinosa* open-pollinated families and populations in the Kaunas, Šiauliai, and Šilutė progeny trials. Families that contributed significantly to the interaction variance are indicated by dark bars and estimates of ecovalences (%) are above the bars. The coefficients of additive variation (CV_A, %) of each population are indicated at the bottom of the bar groups.

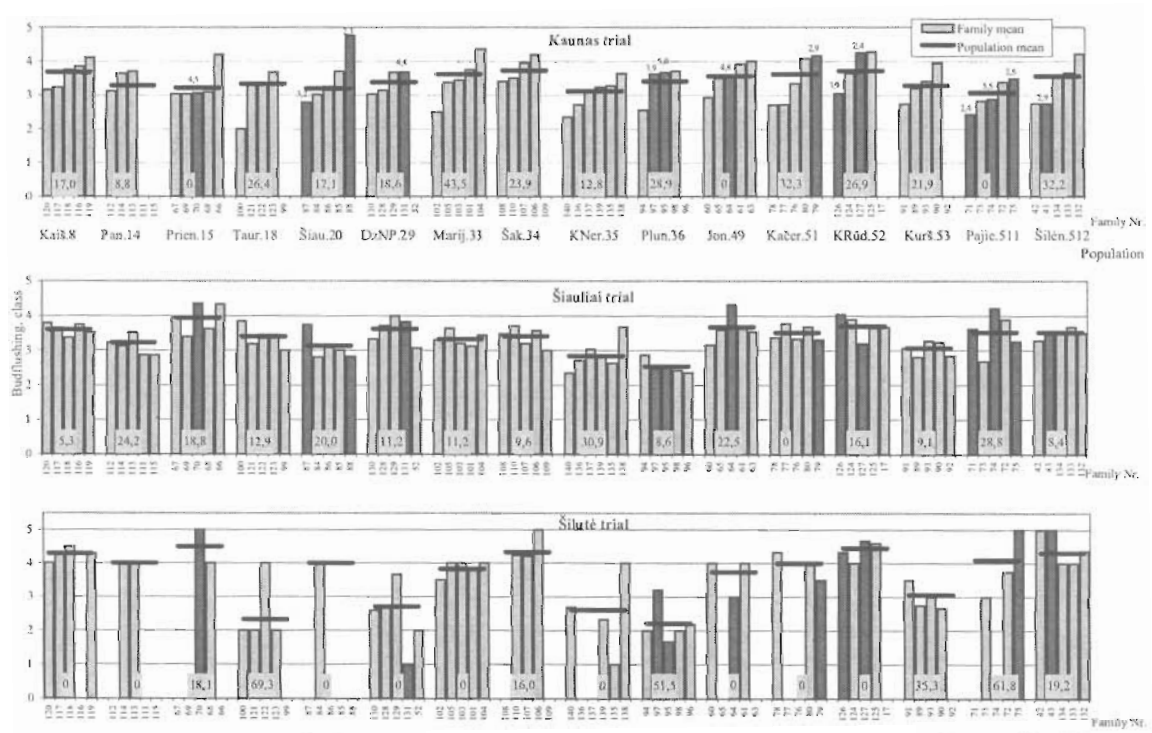

Figure 2. Bud flushing stage of *Alnus glutinosa* open-pollinated families and populations in the Kaunas, Šiauliai, and Šilutė progeny trials. Families that contributed significantly to the interaction variance are indicated by dark bars and estimates of ecovalences (%) are above bars. The coefficients of additive variation (CV_A, %) of each population are indicated at the bottom of the bar groups.

Table 4. Characteristics of stability of height growth of *Alnus glutinosa* open-pollinated families from populations in 3 trials: breeding values, mean breeding values, family means, range of breeding values, coefficient of variation and sum of squared deviations of breeding means across trials.

Population Nr.	Family Nr.	Breeding values in trials, %			Mean breeding value, %	Family mean, cm	Range of breeding values	Coeffic. of variation	Sum of squares of deviations
		Kaunas	Šiauliai	Šilutė					
8	116	-0.47	5.93	.	2.73	102.5	6.40	33.8	20.5
8	117	8.40	-6.55	4.51	2.12	102.1	14.95	43.4	120.3
8	118	-3.42	-9.11	-7.41	-6.65	84.4	5.70	30.2	17.1
8	119	0.50	7.16	2.33	3.33	105.2	6.66	25.9	23.7
8	120	7.55	-10.77	13.34	3.37	94.7	**24.12**	35.8	**317.0**
15	66	18.10	-9.26	.	4.42	92.8	**27.35**	**51.1**	**374.1**
15	67	-6.83	-6.58	.	-6.71	86.3	0.24	31.9	0.0
15	68	-6.89	-21.33	-0.60	-9.61	81.3	20.73	33.8	**225.9**
15	69	-8.06	0.35	.	-3.86	89.7	8.41	33.4	35.4
15	70	2.11	-4.30	-2.30	-1.50	84.7	6.40	**36.0**	21.5
33	101	-3.97	6.71	0.13	0.96	96.5	10.69	31.1	58.1
33	102	-5.19	-1.04	3.67	-0.85	95.3	8.86	23.3	39.3
33	103	14.26	-2.71	-2.30	3.08	113.4	16.97	34.9	187.5
33	104	9.80	-15.64	2.58	-1.08	96.6	**25.44**	**39.5**	**343.7**
33	105	1.81	9.65	-0.25	3.74	105.8	9.91	25.0	54.7
35	135	-12.15	-8.93	-3.15	-8.08	85.6	9.00	28.2	41.6
35	136	-12.02	-19.15	.	-15.59	81.7	7.13	23.7	25.4
35	137	-5.61	1.81	.	-1.90	96.6	7.41	34.6	27.5
35	138	10.37	-10.60	0.25	0.01	95.3	**20.97**	30.9	219.9
35	139	10.19	11.21	1.80	7.73	109.5	13.01	30.9	53.3
35	140	1.89	3.71	9.64	5.08	105.7	7.76	25.8	32.9
36	94	-11.10	-6.92	-3.27	-7.09	83.0	7.83	30.8	30.7
36	95	-1.36	13.75	-2.80	3.20	105.5	16.56	20.2	168.1
36	96	.	21.19	0.48	10.83	111.2	20.71	22.3	214.5
36	97	5.47	4.27	21.27	10.33	109.6	17.00	31.6	180.0
36	98	12.15	15.28	-3.10	8.11	109.0	18.38	19.4	193.4
51	76	-5.53	-5.31	.	-5.42	83.8	0.22	24.8	0.0
51	77	-0.21	-1.83	.	-1.02	94.5	1.62	35.1	1.3
51	78	-1.51	1.75	-2.01	-0.59	93.4	3.76	27.1	8.3
51	79	4.60	9.77	8.14	7.50	106.5	5.18	23.4	14.0
51	80	-2.77	2.24	-3.85	-1.46	98.4	6.10	26.1	21.2

Table 5. Characteristics of height growth stability of *Alnus glutinosa* open-pollinated families over 3 trials: Wricke ecovalences, Shukla stability variances, Finlay-Wilkinson parameters of linear regression equation (interception and regression coefficient), Eberhardt-Russell stability parameter (residual variance). Characteristics indicating lowest stability are highlighted in **bold**.

Population Nr.	Family Nr.	Wricke ecovalence, %		Shukla stability variance			Finlay-Wilkinson/Eberhar.-Russell stability parameters		
		standard	based on breed. values	Variance	F	P	Interception	Regression coefficient	Residual variance
8	116	0.46	0.29	19.9	1.45	0.23	66.9	0.36	.
8	117	1.82	1.70	61.1	3.23	0.04	-119.2	2.24	11.5
8	118	0.84	0.24	8.3	0.33	0.72	-96.2	1.85	15.1
8	119	0.52	0.33	11.6	0.78	0.46	32.4	0.74	33.9
8	120	**23.82**	**4.48**	**161.8**	6.76	0.00	-168.5	**2.85**	**1417.9**
15	66	**20.60**	**5.29**	**382.1**	12.67	0.00	-403.2	**5.25**	.
15	67	1.3	0.00	.	.	.	-21.4	1.11	.
15	68	2.30	3.19	115.2	5.09	0.01	-164.0	2.51	13.5
15	69	2.97	0.50	35.2	1.90	0.17	160.7	-0.73	.
15	70	1.32	0.30	10.5	0.45	0.64	18.8	0.66	99.8
33	101	9.36	0.82	29.3	1.54	0.21	255.6	-1.68	125.4
33	102	0.83	0.56	19.6	0.65	0.52	87.5	0.09	2.2
33	103	**20.7**	2.65	95.5	4.22	0.01	-220.9	3.26	774.9
33	104	**4.41**	**4.86**	**175.5**	7.97	0.00	-208.4	**3.10**	3.6
33	105	1.20	0.77	27.5	0.84	0.43	21.9	0.84	93.1
35	135	2.77	0.59	20.8	1.20	0.30	-49.2	1.32	151.6
35	136	0.51	0.36	25.0	1.44	0.23	-66.1	1.48	.
35	137	0.25	0.39	27.1	1.53	0.22	47.7	0.50	.
35	138	1.80	3.11	112.1	5.78	0.00	-117.4	2.15	18.5
35	139	3.41	0.75	26.8	2.17	0.11	-13.9	1.21	204.9
35	140	1.05	0.46	16.3	1.02	0.36	-45.8	1.59	43.3
36	94	0.32	0.43	15.2	0.77	0.46	15.9	0.71	17.3
36	95	6.09	2.38	85.6	4.20	0.01	131.9	-0.32	317.6
36	96	3.12	3.03	**218.6**	7.25	0.01	371.9	-2.77	.
36	97	**9.29**	2.54	91.6	6.64	0.00	-8.1	1.29	**754.9**
36	98	4.69	2.73	98.5	2.90	0.05	58.1	0.47	311.2
51	76	0.12	0.90	.	.	.	19.7	0.66	.
51	77	0.08	0.02	0.3	0.01	0.90	1.4	0.98	.
51	78	1.68	0.12	3.8	0.21	0.81	121.5	-0.29	6.0
51	79	7.33	0.20	6.7	0.40	0.67	112.9	0.02	**510.2**
51	80	2.85	0.30	10.3	0.62	0.54	70.8	0.24	142.7

Table 6. Genetic correlations between height growth (H), bud flushing (BF), and frost resistance (FR) within and across the progeny trials of *Alnus glutinosa*. Level of significance is denoted by: *- 0.05>P>0.01, ** - 0.01> P>0.001, *** - P<0.001. Correlations within trials are presented in shaded sections.

Trial		Kaunas			Šiauliai			Šilutė		
	Trait	H	BF	FR	H	BF	FR	H	BF	FR
Kaunas	H	-	0.18	0.42***	0.04	0.22	-0.01	0.13	0.00	0.18
	BF		-	0.02	0.13	0.13	0.08	0.07	0.29**	-0.01
	FR			-	0.15	-0.00	0.16	0.22	-0.00	0.11
Šiauliai	H				-	-0.15	0.68***	0.15	-0.10	0.10
	BF					-	-0.26**	-0.21	0.46***	-0.18
	FR						-	0.12	-0.21	0.16
Šilutė	H							-	-0.02	0.53***
	BF								-	-0.02
	FR									-

The variance component of population x environment interaction in variation of bud flushing was significant, however it was the same small scale as the population variance component and comprised up to 9.3%. Only the Prienai (15) and Plungė (36) populations had high and significant Wricke's ecovalences (19.1 and 22.1%). The instability of performance of these populations was also indicated by other characteristics (Table 7 and 8). The most stable time of bud flushing was found for the Kazlų Rūda (52), Kaišiadorys (8), and Kuršių Neringa NP (35) populations. No other traits showed significant *g x e* interaction (Table 2). Only one population (Dzūkija NP) contributed significantly to the *g x e* interaction in height growth with a high and significant ecovalence estimate (Table 8). Ecovalences of the Kuršių Nerija (35), Plungė (36) and Pajiesys (511) populations were close to significance (P=0.07 - 0.08) and were rather high (6.1 - 26.3%). Low stability of these populations was also indicated by large range of variation of breeding values, coefficient of variation and sum of squares of deviations of breeding means across environments (Table 7). However, the highest regression coefficients (one of Finlay-Wilkinson parameters, Table 8) were

Population name /Nr.	Breeding values in trials, %			Mean breeding value, %	Population mean, cm	Range of breeding values	Coeffic. of variation of breeding values	Sum of squares of deviations
	Kaunas	Šiauliai	Šilutė					
Kaišiadorys-8	3.58	-2.39	1.63	0.94	125.9	5.97	18.5	**35.8**
Panevėžys-14	-7.65	-0.45	-0.69	-2.93	118.5	7.20	33.4	30.1
Prienai-15	-2.38	-9.35	-1.45	-4.39	114.3	7.89	**37.2**	**37.9**
Radviliškis-16	1.35	-0.26	0.19	0.43	124.6	1.62	1.4	35.0
Tauragė-18	-2.71	2.52	-1.25	-0.48	121.9	5.22	14.5	30.9
Šiauliai-20	0.04	2.10	-1.75	0.13	128.4	3.84	7.4	34.5
Dzūkija NP-29	8.46	-5.93	-2.55	-0.01	122.6	**14.40**	**113.4**	**35.7**
Marijampolė-33	6.85	-0.23	0.24	2.28	126.3	7.08	31.3	**36.1**
Šakiai-34	3.23	4.23	5.18	4.21	127.2	1.95	1.9	34.1
K.Nerij. NP-35	-1.52	-2.98	3.90	-0.20	122.9	6.88	26.3	32.5
Plungė-36	0.62	9.15	2.49	4.09	126.6	**8.53**	**40.2**	33.4
Jonava-49	1.17	2.12	-0.97	0.78	125.8	3.09	5.0	34.1
Kačerginė-51	-1.62	0.87	1.20	0.15	124.4	2.81	4.7	28.8
K.Rūda-52	-0.74	4.10	-3.91	-0.18	124.2	**8.02**	32.6	30.6
Kuršėnai-53	-2.26	-3.64	-0.31	-2.07	119.0	**8.02**	5.6	29.8
Pajiesys-511	-4.92	0.94	4.11	0.04	120.3	**9.03**	**42.0**	29.8
Šilėnai-512	-1.51	-0.79	-6.05	-2.79	121.2	5.26	16.3	33.4

Table 7. Characteristics of stability of height growth of *Alnus glutinosa* populations' progenies over 3 trials: breeding values in individual trials, mean breeding values, family means, range of breeding values, coefficient of variation and sum of squared deviations of breeding means across trials.

Population name/Nr.	Wricke ecovalence, %		Shukla stability variance			Finlay-Wilkinson/Eberhar.-Russell stability parameters		
	standard	based on breed. values	Variance	F	P	Interception	Regression coefficient	Residual variance
Kaišiadoriai-8	0.35	4.29	9.60	1.34	0.26	2.28	1.00	34.12
Panevėžys-14	**1.49**	7.75	18.05	1.52	0.22	5.12	0.88	**97.91**
Prienai-15	0.49	**8.62**	**20.20**	2.21	0.11	-20.91	1.08	13.88
Radviliškis-16	0.30	0.32	.	.	.	-4.39	1.05	24.23
Tauragė-18	0.62	3.37	7.33	0.77	0.46	0.19	0.97	**52.98**
Šiauliai-20	**5.32**	1.71	3.29	0.44	0.65	-43.54	**1.35**	13.95
Dzūkija NP-29	**1.84**	**26.26**	**63.33**	9.62	0.00	-23.02	**1.21**	**93.17**
Marijamp.-33	1.44	7.26	16.86	1.77	0.17	-15.63	**1.19**	**60.38**
Šakiai-34	0.53	0.44	0.18	0.02	0.98	21.04	0.87	0.83
K.Nerij.NP-35	0.72	6.09	14.00	2.62	0.07	19.30	0.83	12.62
Plungė-36	0.97	**9.31**	**21.88**	2.61	0.07	0.30	1.06	40.42
Jonava-49	0.79	1.16	1.94	0.25	0.78	-13.09	1.10	5.75
Kačerginė-51	0.79	1.10	1.78	0.24	0.79	15.79	0.86	35.73
K.Rūda-52	0.98	3.55	17.57	2.17	0.11	-19.40	1.16	29.72
Kuršėnai-53	0.17	1.29	2.26	0.31	0.74	3.63	0.94	3.34
Pajiesys-511	**2.08**	**9.72**	**22.87**	2.59	0.08	31.97	0.71	19.66
Šilėnai-512	0.94	3.77	8.32	1.29	0.28	-26.87	**1.22**	0.14

Table 8. Characteristics of height growth stability of *Alnus glutinosa* populations' progenies over 3 trials: Wricke ecovalences, Shukla stability variance, Finlay-Wilkinson parameters of linear regression equation (interception and regression coefficient), Eberhardt-Russell stability parameter (residual variance). Characteristics indicating lowest stability are highlighted in **bold**.

found in the Šiauliai (20), Šilėnai (512), Dzūkija NP (29), and Marijampolė (33) populations. Of these populations (Dzūkija NP and Marijampolė) only 2 had a high Eberhardt-Russell stability parameter, residual variance of linear regression (Table 8.).

Discussion

Among environment variation

A large variation in the height growth and bud flushing of progenies among trials (localities) with different environments reflected in the ANOVA's strongly significant effects of the site conditions (block and trial effects) indicated high phenotypic plasticity of Lithuanian black alder populations and families. Block and trial effects indicate consequences of slightly different factors. Block effects reflect the reaction of trees to different edaphic and micro-climatic conditions found within individual progeny trial. Trial effects reflect reaction of trees to the combined effects of edaphic site conditions in a trial, climatic conditions in a trial, and climatic conditions of the given eco-climatic region. High phenotypic plasticity indicates that individual trees in the populations have the ability in the short term to respond to changes of climate and environment. Significant phenotypic plasticity in adaptive traits may be useful under changing conditions in a short timeframe but may be detrimental in a long-term perspective since it means that natural selection cannot operate at full strength (*cf* Eriksson 2000). As to the frost resistance, strongly significant effects of the site conditions in variation of this trait do not indicate the presence of plasticity but rather characterise effects of local climatic factors in regions where progeny trials were established.

Within population genetic variation

Low family variance component estimations found in joint ANOVA (model 1) throughout the 3 test plantations for most traits can result from disturbances in the growth of progenies caused by severe frost damages in lower parts of all progeny trials and poor survival in the Šilutė trial due to competition with vegetation. This increased the random error and genotype x block and genotype x trial interactions. Within individual trials the CV_As for growth and phenology traits in our study were similar to those estimated for other broadleaf tree species (Cornelius 1994 and lit. cit.; Baliuckas et al. 1999, 2000, Baliuckas, Pliūra 2000, etc.). Heritabilities and CV_A for growth and phenology traits studied were generally larger than for stem diameter, frost resistance, and resistance to fungi diseases (Table 3). Also there was a variation in the estimates of the heritability and CV_A dependent on the trial, e.g. heritability coefficient for height varied from 0.43 to 0.70, CV_A varied from 19.5 to 22.0% (Table 3). This variation might be both due to a different scale of growth disturbances in different progeny trials and due to differences in phenotypic plasticity of families. Even on the growth in the 3 trials did not differ much (Table 3), the individual populations differed in CV_A for height, diameter and other traits (Figs. 1-2). The presence of sufficient additive variance in traits of adaptive significance is of greatest significance for the long-term gene conservation (Ritland 1996; Eriksson 2000) and tree breeding. The additive variance within populations in our experiments suggests that all black alder populations have potential for adaptation via natural selection during the juvenile stage if the environmental conditions change.

Contrary to other broadleaved tree species (Baliuckas et al. 1999, Baliuckas, Pliūra 2000) we did not find any significant genetic correlation between the bud-flushing stage and height growth or frost resistance (Table 6). However, the absence of correlations can be due to the fact that spring frost occurred very late and severely damaged the whole stem increment in all our trials when trees had already passed all bud-flushing stages. The adaptive role of phenology in black alder could be clarified by continuing studies on spring frost damages during consecutive years.

Family × environment interactions and stability of families

The significant family x environment interaction variance components found for height growth and phenology (Table 2) indicated the presence of differences among families in adaptedness to different growth conditions. The presence of interaction was supported by very low and insignificant correlation coefficients for the height growth across 3 trials. For bud flushing the genetic correlations coefficients were significant between the Kaunas and Šilutė and between the Šiauliai and Šilutė trials (r=0.29 - 0.46). Insignificant genetic correlation between phenology of families in the Kaunas and Šiauliai trials indicated that ecological conditions in these trials are rather different and helps us reveal specific adaptations of families. The significant genotype x environment interaction for height growth at the population and family levels were also found in recent studies of *Alnus rubra* (Hamann et al. 2000).

Variation of breeding values of families across trials (Table 4) indicates that families differ in stability. These differences were expressed both in the level of plasticity and in the type of plastic response. Every characteristic calculated to evaluate individual plas-

ticity, stability, and reaction norms of families (Tables 4 and 5) characterised different aspects of these features. The range of variation of breeding values have characterised the relative range between the poorest and best performance of families in two contrasting trials. Although this characteristic reflects reaction norms, it is still biased due to variation around the regression line. Meanwhile, the sum of squares of deviations of breeding values characterised relative total variation across all trials. The coefficient of variation of breeding values of individual families gave characteristics of relative total variation across all trials standardized to the grand mean of family.

Wricke ecovalences (both standard, derived from family means and one, derived from breeding values) characterised the relative level of stability of individual families and the contribution of each family to the total *g x e* interaction (family x trial interaction). Shukla's stability variance is related linearly to the ecovalence value (Kang and Miller 1984). The Shukla's method (Shukla 1972) provides a possible method to evaluate its statistical significance. However Shukla's stability variance and Wricke ecovalences are relative characteristics that depend on variation of performance of other families over trials. Absolute stability of families is better characterised by the Eberhardt-Russell (1966) stability parameter, residual variance of linear or polynomial functions. It shows how much site family means deviate from the individual family growth line/curve. High residual variance indicates that families are sensitive not to the general trend of changes in environment but to a specific environment. In calculating residuals the variation of other families is almost not considered. Therefore the results from evaluation of each family by means of Shukla's stability variance or Wricke ecovalences are different from those by residual variance. In our experiment, the highest Wricke's ecovalences and Shukla stability variances (Table 5) indicated that families 66, 104, and 120 contributed most to the total *g x e* interaction. Meanwhile, high residual variance (Eberhardt-Russell stability parameter) indicated that another set of families (families 120, 103, and 36) was most unstable in height growth.

However, Wricke's ecovalences and Shukla stability variances do not directly characterise a reaction norm if the progeny is tested along an ecological gradient. The response of individual families to a gradual change of growth conditions is best characterised by using slope coefficients of linear regression (Finlay-Wilkinson parameter) or by using coefficients of quadratic or other types of equations. The highest coefficients of linear regression (Table 5) indicate that families 66, 103, 104, and 120 were more responsive in growth. High regression coefficients can identify genotypes that benefit from fertile sites and high inputs of nutrients. High interception coefficients identify genotypes that can grow well when nutrients are limited. The regression coefficients of some families presented in Table 5 show different types of responses to the range of environments. Families that have linear regression coefficients of approximately 1.0 have average stability in all environments. These families are 77, 105, and 139 (b = 0.98, 0.84, and 1.21 respectively), which have the lowest ecovalences. The low regression coefficients of families 116, 102, 79, 80, and others indicate high stability and low reaction norms. If growth is considered an indicator of adaptation in the sense of domestic fitness, then the general type of adaptation can be defined based on performance across the range of environments. Families 118, 68, 135, and 94 have below-average height growth in all trials, both in low- and high-yielding environments (Table 4). Thus, they can be defined as poorly adapted to all environments. Meanwhile, the growth of families 103 and 98 was below average on the fertile site (Šiluté trial) but above average on the poor site (Kaunas trial). Thus, they could be defined as specifically adapted to low-yielding environments. Families 101 and 102 exhibited other type of adaptation producing below-average yields on poor sites, but above-average growth under favourable conditions. Therefore, these families can be described as specifically adapted to high-yielding environments.

The levels of reaction norms, instability, and general performance (growth) of families are not always interrelated. For example, families 96, 97, and 79 had the best general growth. However, families 66, 103, 104, and 120 were most responsive to improvement of growth conditions (i.e., they had the highest reaction norms indicated by the highest linear regression coefficient), but ecovalence estimates indicated that these were not among the most unstable families (Tables 4 and 5). This finding corresponds to the hypothesis by A. Bradshaw (1965), C.Schlichting and D.Levin (1984), etc. that phenotypic plasticity can be considered to be a trait in itself which can evolve independently of the trait.

Progenies from different populations exhibited slightly different types of behaviour. The largest differences between families in response to the range of environments were within the most productive populations (Plungė (*36*) and Marijampolė (*33*)). These differences were indicated by a large variation in the sign and the size of regression coefficients. High ecovalence estimates indicate that families from these populations were among the most unstable. In general, all populations consist of families of different adaptation types, reaction norms and stability levels.

Many studies of reaction norms (Knight 1970, Roberds et al. 1976, Gupta and Lewontin 1982, Gregorius and Namkoong 1986, Namkoong et al. 1992) indicated that physiologically reasonable reaction norms estimated as relative response functions to site means, reference genotypes or direct measures of the environment, are non-linear. Therefore, use of non-linear equations can qualify reaction norms more precisely. Large first regression coefficients of quadratic equations can identify families that have the largest reaction norms on the poorest sites along an extended site gradient; large second regression coefficients indicate families in which reaction norms are highest on a range of more fertile sites. However, due to the low number of trials (3) in our studies, evaluating the reaction norms by computing the quadratic parameters of polynomial function was not possible.

Among population variation

The population variance components for most adaptive traits on the 3 progeny trials were very low. This could be explained by both the absence of population differentiation and by a small number of families per population sampled and included into the study. The significant differences in phenology (time of bud flushing) were defined among most populations in the Šiauliai trial. However, in the Kaunas and Šilutė trials, due to the even smaller number of families per population, only distinctive populations were significantly different from each other. Nevertheless, the populations that were the most distinctive in bud flushing kept similar phenological behaviour over different test plantations. Recent studies of *A. sinuata* also showed absence of significant inter-population variation in spring frost hardiness (Benowicz et al. 2000). However, a high inter-population variation was found for winter frost hardiness and biomass production.

The importance of using black alder autochthonous provenances well adapted to habitats has been emphasized by many researchers (Glavac 1962, Weisgerber 1974, Komlenovic and Krstinic 1987, etc.). Recent studies of *A. rubra* show that provenances from locations close to test plantations had superior performance in growth and survival, suggesting the adaptation of the species to local environments (Hamann et al. 2000). However we did not find a clear trend that local populations of black alder performed better in trials which had been established close to their origin. Progeny from only some single populations originating near the trial areas performed better than the average, e.g. the Šiauliai (20) and Plungė (36) populations in the Šiauliai trial or the Marijampolė (33) and Kaišiadorys (8) populations in the Kaunas trial. For height growth only from the 2 to 4 fastest growing populations (the Marijampolė (33) and Šakiai (34) populations in the Kaunas trial and the Plungė (36), Šakiai (34), Kazlų Rūda (52), and Kačerginė (51) populations in the Šiauliai trial) were significantly different from populations that performed most poorly. Considering growth as an indicator of adaptation, the Šakiai (34) and Plungė (36) populations could be defined as populations of general adaptation because they exhibit high growth in all trials (Table 8). Below-average height growth of the Prienai (15), Kuršėnai (53) and Šilėnai (512) populations indicate their low general adaptability. The comparative progeny studies of broadleaved tree species (Baliuckas et al., 1999) indicate that both among population and within population genetic variation of phenology and height growth were lower in *A. glutinosa* than in *Acer platanoides* or *Fraxinus excelsior*. Variation in adaptive traits among populations in our study is positive for developing an efficient gene conservation system of black alder based on the Multiple-Population Breeding System (MPBS) concept that was developed for joint breeding and gene conservation by Namkoong (1984). The results of our studies give primary indications on target populations that can be included into a national network (Pliūra, 1999) of multiple-population gene conservation system of black alder.

Population × environment interactions and stability of populations

The results presented in Tables 7 and 8 indicate that populations differ in level of plasticity and the type of plastic response. The significant variance component of population x environment interaction in variation of bud flushing, which characterise the differences in type of phenotypic plasticity of populations, gives some indication of the possible presence of specific adaptations in phenology. However, only two populations (Prienai (15) and Plungė (36)) had significant and high ecovalence estimates. The presence of specific adaptations should be considered with caution because of the precision problems in estimating the $g \times e$ interaction component in joint analysis of variances resulting from heterogeneous error variance in different trials.

Absence of specific adaptations in growth or frost resistance was indicated by a lack of significant population x environment interaction for these traits. However, the differences in regression coefficients (Table 8) indicate that even in the absence of significant population x environment interaction, populations can differ in reaction norms, response to environment gradient over trials. The most responsive in height growth were the Šiauliai (20), Šilėnai (512), Dzūkija NP (29),

and Marijampolė (33) populations. The significant and high ecovalence estimate of the Dzūkija NP population was also present in the absence of significant population x environment interaction. The results of studies of responses of *A. glutinosa* and other broad-leaved tree populations to climate change by simulating transfers of each population to different locations, enabled us to conclude (Chuine et al. 2000) that local adaptation would probably not be a serious constraint in predicting the phenological responses to global warming.

Conclusions

Large variation in the growth traits and bud flushing of progenies among localities with different environments reflected in strongly significant effects of the site conditions indicated high phenotypic plasticity of Lithuanian black alder populations and families. This means that individual trees in populations have the ability in the short term to respond to environmental changes within the range of environment conditions present in our trials and cope with some of the foreseen consequences of global climate warming. However, it is not clear weather this response is adaptive and enhances plant fitness, or non-adaptive and deteriorates plant fitness. Strongly significant effects of the site conditions in variation and frost resistance did not give an indication of existence of plastic response but rather reflected a rate of negative consequences of unfavourable local climatic factors in some of the locations where progeny trials were established.

Throughout the 3 test plantations studied, the family variance component was relatively low, varying from 2.1 to 3.1%. However, in every test plantation the family variance component was often significant and higher, reaching up to 38.3%. Even though the heritabilities and CV_A for growth and phenology traits varied from site to site, they were generally larger than for other traits. A sufficient amount of additive variance within populations and among population variation suggests that black alder has a potential for adaptation via natural selection during the juvenile stage if environmental conditions change. The presence of genetic variation in frost resistance found in the study shows the possibility of the species to cope with a higher frequency and rate of spring frosts which are predicted as the consequence of global climate warming. However, the negative consequence of this adaptation can be a significant loss of genetic variation both in traits of resistance and growth. Present genetic variation of black alder both at population and family levels also indicates the possibility for genetic gains in selection of the best populations and plus trees, and in developing long-term tree breeding and gene conservation.

The variance component of genotype x environment interaction in variation of different traits indicating the existence of differences among families for their plastic response was rather small, but was larger than the variance component of families. The absence of significant genetic correlation for some traits among trials also indicated that *g x e* interaction plays a significant role in variation of these traits. However, in general the performance of the families across environments was rather stable. Only 16.5% of the families tested contributed significantly to the *g x e* interaction for phenology and 24.7% of families for height growth, and their estimates of ecovalence values were generally low (<5.5%). The level of reaction norms, instability, and general performance (e.g. growth) of families were not always interrelated and each family combined different levels of stability, plasticity, type of plastic response, type of adaptation and level of specialization. The largest differences between families in response to the range of environments were within the Plungė (36) and Marijampolė (33) populations, which were most productive. These differences in plasticity and adaptability should be considered in order to maximise the genetic gain in forest tree breeding. If some of the best performing families are adapted specifically to certain environments, then family selection should be made on an ecological basis, i.e. adequate families should be selected for specific ecological conditions of a given forest eco-region and/or site.

The significant genetic correlation found between the height growth and frost resistance within individual progeny trials indicated that frost negatively influenced the growth. Fast-growing families can better survive and adapt because they are more rapidly passing the stage when trees are most sensitive to spring frosts.

The population variance component for most adaptive traits throughout the 3 progeny trials was rather low. The significant differences in phenology were defined among most populations in the Šiauliai trial. However, due to the smaller number of families per population in the Kaunas and Šilutė trials, only distinctive populations were significantly different from each other. Nevertheless, populations that were most distinctive in bud flushing kept the similar phenology behaviour over different test plantations. For height growth only the 2-4 fastest growing populations were significantly different from the 1-4 populations that performed most poorly. No clear trend was found to support the possibility that local populations of black alder performed better in trials close to the places

of their origin. Progeny from only a few populations that originated close to the trials performed better than average.

The significant variance component of population x environment interactions in variation of bud flushing, which characterise the differences in type of phenotypic plasticity of populations, indicates the possible presence of specific adaptations in phenology. However, only two populations (Prienai (15) and Plungė (36)) had significant and high ecovalence estimates. Even in absence of significant population x environment interactions for growth or frost resistance the differences in regression coefficients indicates that populations differ in response to an environmental gradient over trials. The Šiauliai (20), Šilėnai (512), Dzūkija NP (29), and Marijampolė (33) populations were most responsive in height growth. This variation among populations in adaptive traits is positive for developing an efficient joint breeding and gene conservation system for black alder based on the Multiple-Population Breeding System (MPBS). The results of our studies give primary indications on target populations that can be included into a national network of multiple-population gene conservation system that is under development for black alder.

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ГЕНЕТИЧЕСКАЯ ИЗМЕНЧИВОСТЬ АДАПТАЦИОННЫХ ПРИЗНАКОВ И ЭКОЛОГИЧЕСКАЯ ЧУСТВИТЕЛЬНОСТЬ ЧЕРНОЙ ОЛЬХИ

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Резюме

Восемьдесят пять полусибовых семей ольхи черной (*Alnus glutinosa* L.) из 17 популяций Литвы изучались в 5-летнем возросте в трех исспытательных культурах, заложенных в различных экорегионах Литвы. Цель изучения: а)оценить генетическую межпопулячионную и внутрипулячионную изменчивость адаптационных признаков (роста в высоту, фенологии, чуствительности к заморозкам и др.), б)оценить, как на генетическую изменчивость влияет различные экологические условия и в)оценить стабильность и нормы реакции популяций и семей в различных экоусловиях.

Обнаруженная достоверное влияние эфектов экологических условий на изменчивость признаков означает присутствие высокой фенотипической пластичности и указывает на хорошие возможности ольхи черной реагировать на изменение окружещей среды и климата. Семейный компонент вариации во всем эксперименте был низкий и составил 2,1 - 3,1%. Но в каждых исспытательных культурах семейный компонент вариации достигал до 38,3%. Наследуемость и коефицент адитивной вариации рпизнаков роста и фенологии были выше чем у других признаков и различались в каждой из исспытательных культур. Значительная адитивная меж- и внутрипулячионная вариация указывает на то, что черная ольха имеет хорошие возможности адаптации через натуральный отбор в ювенильном возрасте в случае изменения окружещей среды. Компонент вариации взаимодействия генотипа со средой, указывающий на существование различий между семьями по их пластической реакции, был выше семейного компонента вариации. Несмотря на это, поведение семей в разных условиях окружещей среды было довольно стабильное: только 16,5% семей играло существеную роль в взаимодействие генотипа со средой по признакам фенологии и 24,7% семей - по росту в высоту, а коэффициент эковалентности достигал только до 5,5%. Каждая семья обладала различным уровнем стабильности, пластичности, типом адаптивности и уровнем специализации. Эти разлия должны учитыватся для достижения наивысшей эфективности селекции. Наибольшие различия между семьями по реакции на изменение экологических условий обнаружены в наиболее продуктивных популяциях Плунге (36) и Мариямполе (33). Достоверная генетическая корреляция, установленна между высотой потомства и поврежденностью заморозком, указывает, что заморозки негативно влияет на рост. Во всем эксперименте достоверное влияние эфекта популяций обнаруженно только на изменчивость распускания почек листьев. Популяционнй компонент вариации составил до 8,4%. Тем временем в каждых испытательных культурах в отдельности он составил от 13,8 до 39,8%. Обнаруженная генетическая меж- и внутрипулячионная изменчивость адаптационных признаков благоприятна для создания эфективной многопопуляционной системы сохранения генетических ресурсов черной ольхи совместно со селекции

Ключевые слова: *Alnus glutinosa,* черная ольха, популяции, семьи, генетическая изменчивость, наследуемость, генетическая кореляция, фенотипическая пластичность, нормы реакции, адаптация