WITHIN-POPULATION VARIATION IN JUVENILE GROWTH RHYTHM AND GROWTH IN *FRAXINUS EXCELSIOR* L. AND *PRUNUS AVIUM* L.

Virgilijus Baliuckas[1], Tomas Lagerström[2] &, Gösta Eriksson[3]

[1] Department of Forest Genetics and Reforestation, Lithuanian Forest Research Institute, Girionys 4312, Lithuania
[2] Department of Landscape Planning, SLU, SE–75007 Uppsala, Sweden
[3] Department of Forest Genetics, SLU, SE–75007 Uppsala, Sweden

ABSTRACT

The purpose of our investigation was to estimate genetic parameters for early growth and growth rhythm traits in *F. excelsior* L. and *P. avium* L. by analysing open pollinated families from four Swedish populations of each species. The populations were sampled along a climatic gradient in southern Sweden. *Fraxinus excelsior* L. was represented by 20–29 open pollinated progenies per population while *Prunus avium* L. had 22–29 families per population. The seedlings were planted in common garden experiments and assessments of growth rhythm and growth were made repeatedly over years up to age 5. Large and significant family effects were obtained for all traits. Generally, the coefficients of additive variance were large. The site × family interaction in *Prunus avium* was slightly larger than in *Fraxinus excelsior*. The genetic correlations between the observations of the same trait during different years were generally strong. As expected there was generally a negative relationship between growth cessation and plant height. The large coefficients of additive variation in separate populations for the adaptive traits studied, indicate a potential to respond to strong environmental changes such as are predicted by global warming. It also indicates good prospects for gene conservation and tree breeding.

Keywords: *Fraxinus excelsior, Prunus avium*, common garden experiments, juvenile age, adaptive traits, gene conservation.

INTRODUCTION

SOULÉ and MILLS (1992) stated that gene conservation is justified for one reason only; the promotion of the fitness of gene resource populations. This agrees with the statement by ERIKSSON *et al.* (1993) that creation of good conditions for future evolution is the most important objective in forest tree gene conservation. A large additive variance within populations for adaptive traits is the best guarantee for future adaptation. Unfortunately, genetic studies of adaptive traits were mainly restricted to the commercially most important species to the neglect of less important species. Thus, there is a great need to fill this gap.

Several scientists have addressed the question of the importance of life history traits on the genetic structure (*e.g.* HAMRICK *et al.* 1992, GOVINDARAJU 1988). The latter reviewed the impact of pollination pattern on genetic differentiation among populations and found the largest gene flow for wind-pollinated species and the lowest for self-pollinated species. The entomophilous plants took an intermediate position. A substantial gene flow increases the effective population size and thereby counteracts genetic drift.

Some life history traits of *Fraxinus excelsior* and *Prunus avium* are presented in Table 1. Both are intermediate species with respect to stage in the ecosystem and have their northern limit of distribution at approximately latitude 60° in Sweden. The major

difference between the two is the pollination vector, wind and insects, respectively. *P. avium* is mainly pollinated by bees. As a consequence of the difference between pollen vectors of the two species, it is assumed that genetic drift will be somewhat higher in *P. avium* than in *F. excelsior*. Our hypothesis is that the additive variance of adaptive traits will be smaller in *P. avium* than in *F. excelsior*.

In *Picea abies* bud flushing and growth cessation are of adaptive significance (cf. DIETRICHSON 1969). It is expected that these traits are also of adaptive significance in other tree species from high latitudes. Since the lowest temperatures are found close to the ground, these growth rhythm traits are of greatest significance during the juvenile phase (cf. PERTTU 1981).

In *Fraxinus excelsior* there are a few provenance studies (WEISER 1974, 1995, GIERTYCH 1995, KLEIN-SCHMIT *et al.* 1996) but within-population estimates of genetic parameters are not known to us. High estimates of additive variance and clone × site interaction were reported for height growth up to age 7 by MURANTY *et al.* (1998), who studied a diallel mating with 14 *P. avium* parents.

The purpose of our investigation was to estimate genetic parameters for early growth and growth rhythm traits in *F. excelsior* and *P. avium* by analysing open pollinated families from four Swedish populations of each species. HOULE (1992) strongly argued for the presentation of the additive genetic coefficient of

Table 1. Some differences in ecological features between F. excelsior and P. avium.

Fraxinus excelsior	Prunus avium
• .wind pollinated;	• .insect pollinated (strictly outcrossing);
• .comparatively dense distribution over large scale of environments including marginal areas of northern distribution;	• .scattered distribution, especially in marginal areas of northern distribution on well drained calcareous sites;
• .seed dispersal by wind and animals;	• .early fruiting and seed dispersal by animals;
• .dioecious or trioecious with changing sex of trees;	• .perfect flowers;
• .highly shade tolerant at young age, up to 30 years;	• .medium shade tolerant at young age;
• .tree recovering via sprouts up to old age;	• .tree recovering via sprouts up to middle age;
• .comparatively long life cycle.	• .comparatively short life cycle;

Table 2. Geographical data of the sampled populations.

No.	Location	Number of families	N. Latitude	E. Longitude	Altitude m a.s.l.
		Fraxinus excelsior			
1	Månkarbo	20	60° 12'	17° 24'	50
2	Tysslinge	29	59° 18'	15° 00'	80
3	Björkerum	28	56° 43'	16° 40'	20
7	Tångdala	30	55° 39'	14° 00'	60
		Prunus avium			
1	Mariestad	24	58° 36'	13° 45'	100–150
2	Drottningkullen	22	58° 28'	13° 43'	130–150
3	Ydre	24	57° 45'	15° 25'	200–250
4	Stenshuvud	28	55° 40'	14° 16'	10–90

variation (CV_A) in quantitative genetics studies since it gives information on the ability to respond to selection as well as the maintenance of genetic variability. Therefore, we present estimates of CV_A besides presentations of variance components.

MATERIALS AND METHODS

Open pollinated families of trees from four Swedish native populations of Prunus avium and Fraxinus excelsior were included in the study. Trees having superior phenotype were selected as mother trees according to strict directives by Tomas Lagerström. The geographic data of the populations and the number of open pollinated families in each population are presented in Table 2. The four populations represent the distribution area of the two species in Sweden. The distance between the trees was 30–40 meters for F. excelsior, while it was 40–50 m for P. avium. These distances were used to avoid any relationship of the trees. One P. avium population, Ydre, had a low population density while Drottningkullen had a high population density, especially uncommon for such a

northern origin.

The seeds were stratified before sowing. Two common garden experiments were established, one in the Uppsala region (Lugnet 58°38') and the other on Öland (56°38'). The P. avium experiments were established in autumn 1993 with 1-year-old seedlings. The F. excelsior experiments were established in autumn 1995 with 1-year-old seedlings. A split-plot experimental design was used with all families of one population kept in a big sub-block, which in turn had six replications of randomized six-tree plots at a spacing of 1 × 1.2 m between trees. (A prerequisite from the funding organisation was that the experiments could be converted to seedling seed orchards; for this reason mixing of populations were not permitted).

The recordings were done during several years and the same measurements of traits were not always recorded at both field experiments. The reason for this was that voles and bad weather caused great losses to the material at the northern site (Lugnet). The number of assessments per season is evident from Tables 3–4. The traits, except for height and diameter, were recorded in classes with linear scales as far as possible.

The traits assessed for *F. excelsior* and *P. avium* were: bud flushing (0–5), leaf autumn colouring (0–4), or leaf fall (1–5), autumn frost damage (0–3) and height. In addition, diameter at breast height was assessed in *P. avium*. The higher the figure the more advanced the stage or colour intensity, or degree of leaf fall or degree of frost damage. The recordings were made up to age 5 in both species.

Statistical methods

Different sets of traits (some being assessed three consecutive years) for each species were used in the statistical analysis. Plot means were used in the ANOVAs while individual observations were used in the calculations of genetic correlations.

Plot means were used in the ANOVAs, type III SS within PROC GLM of SAS Software Release 6.12. PROC MIXED and the REML option were used for computing of variance components.

The transformations of data used for analysis of variance on family plot mean level were: arcsin (x/x_{max}) – for traits assessed in classes, where x = plot mean value, x_{max} = maximal trait value; log x – for traits having metric values. The two models used in the analysis of variance were:

$$y_{iklm} = \mu_o + s_i + b_{k(i)} + f_l + (sf)_{il} + \varepsilon_{iklm} \qquad [1]$$

where: μ_o – is the grand mean, s_i – site effect as fixed, $i = 1, 2, b_k(_l)$ – effect of block within site as fixed, $k = 1,..., 6, f_l$ – family effect, $l = 1,...,$ 20–29 (the numbers of open pollinated families/population varied), $(sf)_{il}$ – the effect of interaction between site and family, ε_{iklm} – the error term. The data from the two sites were pooled in model 1.

$$y_{kl} = \mu_o + b_k + f_l + \varepsilon_{klm} \qquad [2]$$

where: μ_o – is the grand mean, b_k – effect of block, $k = 1,..., 6, f_l$ – effect of family, $l = 1,...,20–29$ (the numbers of open pollinated families/population varied), ε_{kl} – the error term. Model 2 was applied for separate analyses of populations.

The following formula was used in the calculation of additive genetic coefficients of variation:

$$CV_A = \frac{\sqrt{4\sigma_f^2}}{\bar{x}} \cdot 100 \qquad [3]$$

where σ_f^2 – family variance component, $\bar{x}$ – the phenotypic mean of the trait.

Genetic correlations were calculated separately for each population. Correlations were not calculated when the standard error of the family variance component

exceeded 60 % of the estimate of the component. The following types of genetic correlations were carried out:

•• Correlations between the same trait assessed in two or more years.
•• Correlations between different traits assessed in a specific year
•• Correlations between the same trait assessed in the two experiments in a specific year

For calculations of genetic correlation coefficients at the individual level the set of programs "Dfprep" and "Dxmux" of DFREML Software 3.0 a (MEYER 1997) was used.

RESULTS

The observed family variation for each type of trait, bud flushing, growth cessation (leaf colouring or leaf fall), and plant height, is illustrated for one assessment in the two species (Fig. 1–2). These figures reveal that the ranking of the families varies among the traits.

As seen from Tables 3–4, the percentage variance components for families and the corresponding CV_A for individual populations at the two test sites are with some exceptions relatively high in both species. Especially high CV_A were observed for autumn frost damage in *P. avium* at the Öland experiment. In three of the four *F. excelsior* populations the variance component for height dropped from year 3 to year 5. In *Prunus avium* there was a trend in the opposite direction. The mean CV_A for height over ages and sites of the northern *F. excelsior* populations were somewhat higher than for the two southern populations (Figure 3). The corresponding estimates for *P. avium* did not show any clear trend.

In *F. excelsior* the family × site interaction was much smaller in 6 of 11 cases than the family component (Table 5). In contrast, the family × site interaction was more important than the family effect in *P. avium* (Table 6). The interaction was especially pronounced for height in *P. avium*.

The within-trait genetic correlations between years were strong for bud flushing and plant height in *F. excelsior* (Table 7). The few between-trait correlations in *F. excelsior* were weak or negative with one exception (bud flushing and height in population, Tysslinge, 59°18', $r_g = 0.97$). The within-trait genetic correlations between years were strong in *P. avium* (Table 8). The strong negative relationships between height and leaf colouring as well as between diameter and leaf colouring in *P. avium* is worth mentioning (Table 8).

Bud flushing was the only genetic correlation between the two experiments that could be calculated for *P. avium* and only for one population, Stenshuvud, 55°40', with a low coefficient, 0.11 ± 0.28.
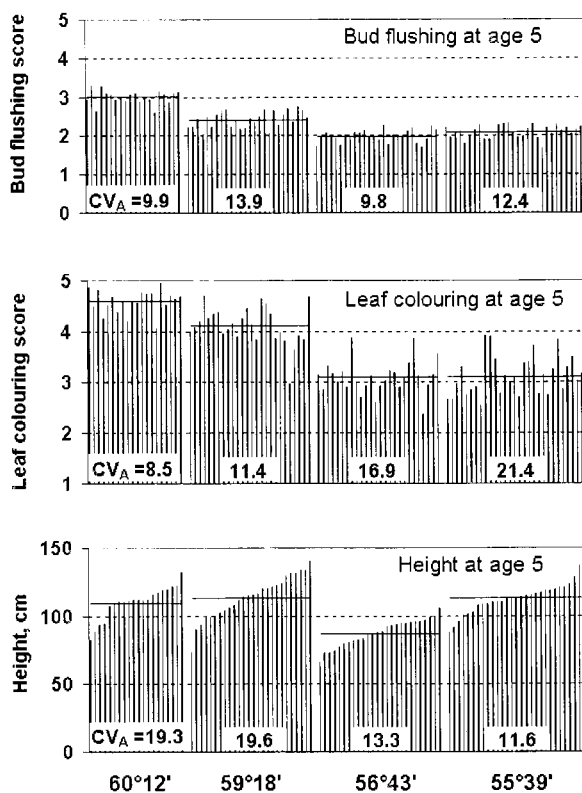
Figure 1. Variation in bud flushing at age 5 (score from 0 with no bud burst to 5 with fully developed leaves), leaf colouring at age 5 (score 1 with no leaf fall to 5 with all leaves fallen) and height at age 5 among open pollinated families of four Swedish *Fraxinus excelsior* L. populations (see latitude) at field trial (lat. 56°38′, Öland). CV_A for the four populations and traits are indicated.
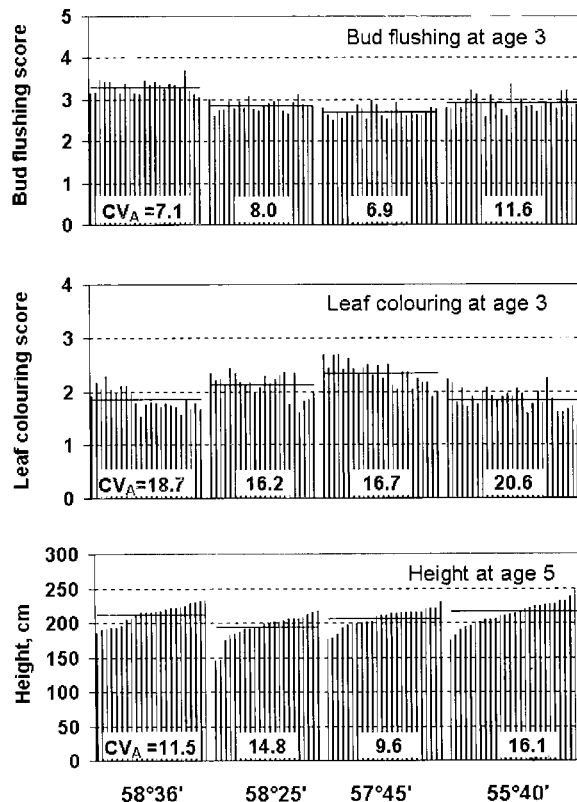
Figure 2. Variation in bud flushing at age 3 (score from 0 with no bud burst to 5 with fully developed leaves), leaf colouring at age 3 (score 1 with no leaf fall to 5 with all leaves fallen) and height at age 5 among open pollinated families of four Swedish *Prunus avium* L. populations (see latitude) at field trial (lat. 56°38′, Öland). CV_A for the four populations and traits are indicated.

DISCUSSION

The original intention to study the same populations of the two species at two sites with different climatic conditions partly failed owing to calamities, mainly voles, damaging the material at the northern site, Lugnet. This study is part of a larger study including *Fagus sylvatica* and *Quercus robur* including more than 23,000 plants. Therefore, recordings of growth rhythm could not be carried out at several occasions. This meant that all recordings did not hit the most appropriate time for revealing genetic differences in growth rhythm traits, *ie* with a median value close to 2.0 or 2.5 depending on the scale used. Growth cessation was originally estimated from leaf colouring but later we had to estimate it from leaf fall since leaf fall started before all leaves had changed colour.

Within-population variation or family effects

As seen from Tables 3–4, most CV_A suggest strongly that improvement by selection will be possible. The first observation at age 4 for bud flushing in *F. excel-*

sior populations is probably exaggerated owing to an early recording of this trait. The same might be the case for the first recording of bud flushing of *P. avium* at age 3 in the Öland experiment. The CV_A were slightly higher in *F. excelsior* than in *P. avium*. Noteworthy is the high CV_A for autumn frost damage in *P. avium*, which suggests that there are great possibilities for improvement of this trait. JANSSON *et al.* (1998) reported CV_A of the same magnitude as ours for growth traits of *Pinus sylvestris* cultivated in a growth chamber. Our values are higher than the median CV_A presented by CORNELIUS (1994) in his review article of CV_A in forest tree species, with a strong overweight of conifers.

The drop in CV_A over time for tree height in *Fraxinus excelsior* (Table 3) may be attributed to maternal effects that are most important during the first year.

The growth rhythm traits had mostly high estimates of family variance components in both species. However, the growth cessation traits of the *F. excelsior* populations, 56°43′ and 59°18′, had low estimates at ages 3 and 4. Low estimates are obtained if the assess-

Table 3. Family variance components ± standard errors and coefficients of additive variance in *Fraxinus excelsior* populations according to ANOVA model 2 (1ˢᵗ ass means first assessment at that age).

Variables (age)	Öland (Torslunda)								Lugnet							
	60° 12'		59° 18'		56° 43'		55° 39'		60° 12'		59° 18'		56° 43'		55° 39'	
	σ_f^2	CV_A	σ_f^2	CV_A	σ_f^2	CV_A	σ_f^2	CV_A	σ_f^2	CV_A	σ_f^2	CV_A	σ_f^2	CV_A	σ_f^2	CV_A
Bud flushing																
3	0.6±6.1	3.4	14.1±8.7	13.4	4.2±6.1	9.1	5.5±6.0	14.0	23.6±12.5	14.0	49.0±16.6	22.3	.	.	30.0±11.2	19.8
4 (1st ass.)	16.8±10.2	34.1	41.7±14.8	53.4	5.3±6.3	64.5	16.1±8.2	38.8	.	.	.	.	.	.	.	.
4 (2nd ass.)	18.0±10.5	11.0	49.1±16.5	24.1	28.7±11.6	29.0	26.1±10.4	16.5	.	.	.	.	.	.	.	.
5 (1ˢᵗ ass.)	28.4±13.2	15.1	24.3±11.0	12.7	22.2±10.1	20.1	19.4±8.9	13.3	.	.	.	.	.	.	.	.
5 (2nd ass.)	26.1±12.6	9.9	23.7±10.5	13.9	9.1±7.1	9.8	21.5±9.4	12.4	.	.	.	.	.	.	.	.
Autumn leaf colouring																
3	20.1±11.0	44.4	1.8±5.8	11.7	2.1±5.6	5.6	12.7±7.5	30.0	7.0±8.4	15.6	4.2±6.2	40.4	13.4±8.1	64.1	0.2±4.9	5.2
Defoliation																
4	15.9±9.9	11.4	3.1±6.1	9.1	3.0±5.8	12.5	7.7±6.4	20.9	.	.	.	.	.	.	.	.
5	31.0±13.9	8.5	9.4±7.2	11.4	19.7±9.5	16.9	28.0±10.8	21.4	.	.	.	.	.	.	.	.
Autumn frost																
4	.	.	.	.	.	.	.	.	19.5±11.3	26.5	7.3±6.9	8.7	10.7±7.5	18.4	20.1±9.1	26.8
Height																
3	31.7±14.1	22.9	30.7±12.5	27.2	26.8±11.1	20.3	12.1±7.4	17.1	63.4±23.3	41.8	42.5±15.2	33.1	41.2±14.5	30.6	37.2±12.8	31.3
4	27.4±12.9	19.2	30.5±12.4	23.7	10.8±7.5	15.7	12.8±7.5	14.9	.	.	.	.	.	.	.	.
5	30.0±13.6	19.3	21.2±10.2	19.6	7.6±6.8	13.3	75±6.4	11.6	.	.	.	.	.	.	.	.

ment takes place very early or very late. Two of the assessments took place late, which might partly explain low estimates of the family components.

It should be remarked that high estimates of family variance components may be obtained if matings mainly occur within small cohorts of trees in a population. High estimates may also be obtained if there is a substantial gene flow mediated by birds. Studies of mating patterns in populations of the two species ought to be carried out to complement the results from our investigation.

HANNRUP (1999) discussed different combinations of low and high heritabilities and low and high CV_A. To get some information on short-term (family variance component) and long-term (CV_A) available additive variance we compared the family variance component and its corresponding CV_A for different traits (original data in Tables 3 and 4). When the CV_A was within the family variance component ± its standard error, this was regarded as equal magnitude of the two estimates. With this classification, CV_A and family variance

components were equal for height in 24 of 27 cases, the three deviations coming from *P. avium*. For growth rhythm traits in *P. avium*, 10 of 24 had lower CV_A than variance components. In contrast, 12 of 38 had higher CV_A than variance components in *F. excelsior*, autumn colouring being mainly responsible for this. Only 5 had lower CV_A than variance components in *F. excelsior*.

As regards height, there is no big difference between short-term and long-term possibilities for gene conservation and breeding in the two species. As regards growth rhythm, and especially growth cessation, the possibilities for long-term change are at least as good as for short-term change in *F. excelsior*. In contrast, the prospects for a long-term change of growth rhythm traits in *P. avium* must be regarded as smaller. It should be noted that the estimates of the family variance components are generally higher in *P. avium* than in *F. excelsior* (Tables 3 and 4).

The somewhat higher CVA estimates of the two northern *F. excelsior* populations (Table 3) suggest that populations close to the edge of the northern distribu-

Table 4. Family variance components ± standard errors and coefficients of additive variance in Prunus avium populations according to ANOVA model 2 (1st ass. means first assessment at that age).

Variables (age)	Öland (Torslunda) 58° 36' σ_f^2	CV_A	Öland 58° 28' σ_f^2	CV_A	Öland 57° 45' σ_f^2	CV_A	Öland 55° 40' σ_f^2	CV_A	Lugnet 58° 36' σ_f^2	CV_A	Lugnet 57° 45' σ_f^2	CV_A	Lugnet 55° 40' σ_f^2	CV_A
Bud flushing														
3 (1st ass.)	22.1±11.0	15.3	45.5±22.4	30.9	24.7±11.4	20.0	38.1±13.5	31.9	9.8±8.8	14.0	10.9±12.9	26.0	13.4±9.9	12.3
3 (2nd ass.)	20.9±10.7	7.1	17.4±13.0	8.0	15.4±9.2	6.9	37.3±13.3	11.6	5.8±7.8	5.7	0.0±0.00	0.0	32.8±14.9	12.9
4 (1st ass.)	25.3±11.8	9.1	21.3±14.3	11.8	21.0±10.5	8.7	25.4±10.6	17.8	.	.	.	.	.	.
5 (2nd ass.)	4.5±6.7	10.9	5.2±9.2	14.4	16.4±9.3	18.7	34.7±12.7	50.6	.	.	.	.	.	.
Autumn leaf colouring														
3 (1st ass.)	34.3±14.1	18.7	23.8±15.2	16.2	38.9±14.9	16.7	33.1±12.4	20.6	.	.	.	.	.	.
3 (2nd ass.)	34.8±14.2	12.1	.	.	31.4±13.1	8.9	48.6±15.9	18.7	.	.	.	.	.	.
Autumn frost damage														
4	27.6±12.3	56.1	24.3±15.2	52.9	42.8±14.6	54.0	26.5±11.9	62.4	.	.	.	.	.	.
Diameter														
6	22.7±11.2	13.2	12.4±11.8	14.6	20.6±10.4	15.0	22.2±9.9	20.8	.	.	.	.	.	.
Height														
2	12.1±8.5	9.4	.	.	.	.	.	.	.	.	.	.	.	.
3	17.7±9.9	7.9	31.9±17.8	19.4	12.3±8.4	7.9	16.4±8.7	12.1	7.5±8.2	21.2	.	.	10.7±8.9	28.3
4	.	.	.	.	.	.	.	.	.	.	.	.	15.8±10.1	25.3
5	31.9±13.4	11.5	23.2±15.8	14.8	16.6±9.4	9.6	24.1±10.4	16.1	.	.	.	.	.	.

Table 5. Family and family × site interaction variance components ± standard errors and significances of family and family by site interaction in Fraxinus excelsior populations at age 3. Significances of the family and family × interaction were obtained by ANOVA, model 1 in Materials & Methods.

Traits	Source of variation	Månkarbo		Tysslinge		Björkerum	Tångdala	
Bud flushing	Family	7.4 ±5.0	**	27.8 ± 10.1	***	no data	3.5 ± 5.5	***
	Site × family	0		0			11.2 ± 6.9	**
Autumn leaf colouring	Family	13.7 ± 9.6	**	0.7 ± 4.0		0.1 ± 4.1	0	
	Site × family	4.8 ± 7.2		1.8 ± 5.5		4.5 ± 5.9	11.0 ± 5.0	***
Height	Family	32.0 ± 13.3	***	30.0 ± 11.8	***	14.0 ± 9.7	***	18.8 ± 6.8	***
	Site × family	4.7 ± 5.3	**	5.6 ± 4.9	*	21.6 ± 9.2	***	0.00	

Table 6. Family and family × site interaction variance components ± standard errors and significances of family and family by site interaction in *Prunus avium* populations at age 3. Significances of the family and family × site interaction were obtained by ANOVA, model 1 in Materials & Methods.

Trait	Source of variation	Populations					
		Mariestad		Ydre		Stenshuvud	
Bud flushing (the 1ˢᵗ and the 2ⁿᵈ assessments)	Family	8.6 ± 6.8	***	0		6.0 ± 10.0	***
	Site × family	5.9 ± 6.9		11.5 ± 6.6	0	22.0 ± 11.3	***
Autumn	Family	6.6 ± 6.3	**	0		3.9 ± 10.2	***
	Site × family	4.7 ± 6.7		4.8 ± 5.3		30.6 ± 12.8	***
Height	Family	0		no data		0	
	Site × family	15.0 ± 6.8	***			13.9 ± 6.1	**

Table 7. The range of within-trait and between-trait genetic correlation coefficients ± standard errors for individual populations of *Fraxinus excelsior* at the Öland experiment (See also Materials and Methods).

Group of traits	Bud flushing		Leaf flushing		Coloring	
	min	max	min	max	min	max
Bud flushing	0.62 ± 0.11	1.0 ± 0.03	−0.03 ± 0.13	0.05 ± 0.13	−0.4 ± 0.16	0.97 ± 0.12
Leaf colouring					−0.57± 0.10	0.05 ± 0.13
Height					1.0 ± 0.01	1.0 ± 0.01

Table 8. The range of within-trait and between-trait genetic correlation coefficients ± standard errors for individual populations of *Prunus avium* at the Öland experiment (See also Materials and Methods).

Group of traits	Bud flushing		Leaf colouring		Frost damage		Diameter		Height	
	min	max	min	max	min	max	min	max	min	max
Bud flushing	0.35±0.13	0.94±0.04	−0.51±0.11	0.4±0.14	−0.84±0.07	0.16±0.11	−0.28±0.15	0.67±0.12	−0.32±0.14	0.74±0.08
Leaf colouring			0.90±0.06	0.97±0.03	0.27±0.13	0.78±0.14	−0.92±0.06	−0.81±0.07	−0.89±0.06	−0.69±0.07
Frost damage					0.81±0.09	−1.0±0.14	−0.41±0.14	−0.88±0.06	0.15±0.11	
Diameter							0.84±0.05	0.95±0.02		
Height									0.92±0.03	

tion of this species are at least as variable as more central populations of this species. A similar trend was also found in our previous study (BALIUCKAS *et al.* 1999). This conflicts with the expectation that populations at the margin of the distribution are small and that genetic drift is presumed to be important (STERN and ROCHE 1974). The explanation for our result is probably that our populations are at a distance from the northern limit of the distribution of the two species, and as a corollary of that, genetic drift has been of low importance. Moreover, our data derive from one harvest; flowering and weather condition might influence the mating pattern.

Family × site interaction

There was a tendency to a greater impact of the family × site interaction in *P. avium* than in *F. excelsior* (Tables 5–6). This suggests that specific adaptation to different site conditions plays a larger role in *P. avium* than in *F. excelsior*. However, the number of estimates was low, which may have influenced this result.

For tree height in *P. avium* the family × site interaction was strongly significant (Table 6), which erased the family effect. MURANTY *et al.* (1998) also reported a greater impact of the family × site interaction than family effect for tree height in their study of a *Prunus avium* diallel. The ratio family/family × site amounted
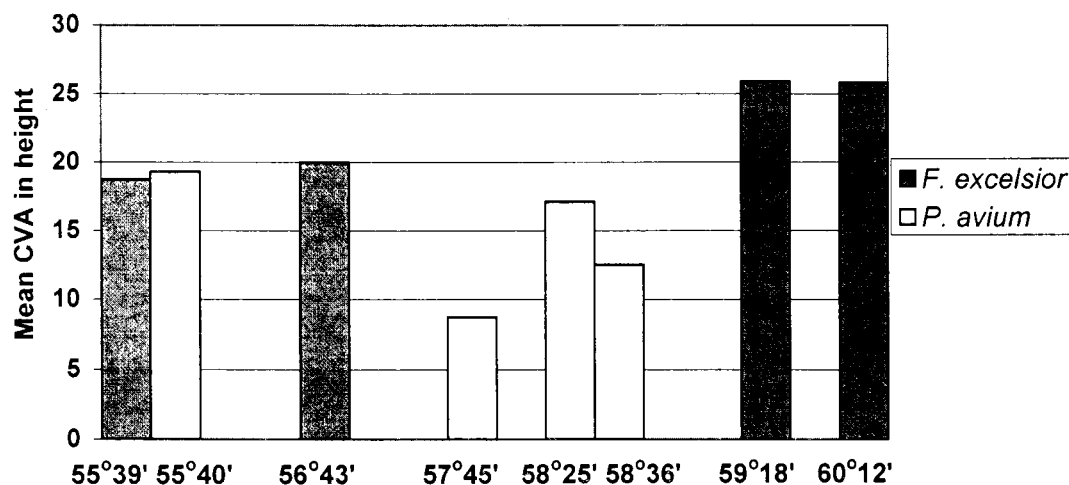
Figure 3. The mean values of coefficients of additive variance for juvenile height of the four populations of each of *Fraxinus excelsior* and *Prunus avium*.

to 1.6. The harsher environmental conditions at our northern experimental location may be responsible for the larger impact of interaction in our study.

Genetic correlations

The stability of bud flushing and height between the recordings at different occasions in *F. excelsior* is evident from Table 7. The mean value of all correlation coefficients was 0.82 for bud flushing. This suggests that assessments in one year might be satisfactory for obtaining the ranking of families of *F. excelsior* during one of the most sensitive phases of the lifetime.

The genetic correlations for bud flushing in *P. avium* were generally somewhat lower than in *F. excelsior* (Table 8). The mean value was estimated at 0.60. The high values for leaf colouring were expected since they originate from two assessments during one year. The minimum value of -0.84 in r_g between bud flushing and frost damage means that the early flushing plants were most frost damaged. The strong and negative relationship between leaf colouring and the two growth traits in *P. avium* is a reflection of the general phenomenon that early growth cessation is strongly related to poor growth (see *e.g.* VELLING 1979). Mainly there was a negative relationship between frost damage and growth traits.

Except for the Björkerum population ($r_g = 0.42 \pm 0.21$) the low importance of family by site interaction for height in *F. excelsior* (Table 5) is reflected in the high correlation coefficients 0.76–0.96 for this trait between the two experiments. The low correlation coefficient for bud flushing between the two experiments ($r_g = 0.11 \pm 0.28$) in the Stenshuvud population is reflected in the comparatively strong family × site interaction component for the Stenshuvud population of *P. avium* (Table 6).

Implications for gene conservation

Under fast environmental change such as is expected in the event of global warming, a large phenotypic plasticity may be needed to cope with change in a short-term perspective while there are two options in a long-term perspective, migration or adaptation via natural selection (cf. ERIKSSON 1999). Many ecologists seem to agree that the change under global warming is faster than any tree migration rates in the past (DAVIES 1988). The large CV_A for the adaptive traits studied means that our two species have a potential to respond to strong environmental changes such as are predicted by global warming. The large CV_A also means that improvement by breeding is possible. Combined breeding and gene conservation could be sensibly carried out with the existing material as a starting point.

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