

WITHIN-POPULATION VARIATION IN JUVENILE GROWTH RHYTHM AND GROWTH IN *QUERCUS ROBUR* L. AND *FAGUS SYLVATICA* L.

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Received April 3, 2001, accepted August 31, 2001

ABSTRACT

The study was conducted to evaluate the genetic parameters in adaptive and growth traits within five Swedish populations of *Quercus robur* L. and three populations of *Fagus sylvatica* L. The *Quercus robur* populations had 27–30 families in each, sampled at latitudes 55° 34' to 60° 12' and the *Fagus sylvatica* populations had 28–30 families in each, sampled at latitudes 55° 28' to 57° 33'. The 1-year old seedlings of *Quercus robur* were planted in nursery experiments at two distant sites at latitudes 59° 40' and 56° 38'. The 1-year old seedlings of *Fagus sylvatica* were planted only at the southern site. The plants were assessed yearly at ages 3–6 and some years twice for growth rhythm traits. Large and significant family effects were obtained for all traits, except for growth cessation and height in some *Fagus sylvatica* populations. Large coefficients of additive variation were obtained. The family × site interaction in *Quercus robur* populations was more pronounced for growth cessation and height, than for bud flushing with a larger family × site component for the southern populations. Stable and strong genetic correlations were obtained for bud flushing in different years and weaker, but stable correlations for growth cessation. Bud flushing and height genetic correlations showed a tendency to change with age from positive or slightly negative to negative. This trend was most pronounced in *Quercus robur* populations. These correlations were almost always negative in *Fagus sylvatica* populations. Late growth cessation was correlated with height. Thanks to the large and significant family effect, all populations in both species demonstrated high potential for adaptation and long-term breeding, which is most beneficial for gene conservation.

Keywords: *Quercus robur*, *Fagus sylvatica*, nursery experiments, juvenile age, adaptive traits, growth rate, gene conservation.

INTRODUCTION

Gene conservation of forest trees was given priority by European politicians during the 1990s. As a result of this, EUFORGEN (European Forest Genetic Resources) networks were established (cf. Anonymous 2000). One of the networks is targeted for deciduous *Quercus* species and *Fagus sylvatica*. Gene conservation requires knowledge of genetic variation within and among populations. The prime objective in gene conservation is to safeguard the potential for adaptation (ERIKSSON 2001). This means that gene conservation methods should be designed such that they enable a target species to respond adequately to any possible changes in the environment. The best way to match the prime objective in gene conservation is to encompass the existing variation in adaptive traits of a species by applying the *Multiple Population Breeding System* suggested by NAMKOONG *et al.* (1980) when gene resource populations are sampled. Gene resource

populations sampled in this way should be used as starting material for dynamic gene conservation (cf. ERIKSSON *et al.* 1993). Future adaptation and speed of adaptation of a species depend on the amount of additive variance for adaptive traits in its gene resource populations. Currently many forest tree gene conservationists are concerned about global climate change. There are examples of tree species with great potential for adaptation. Thus, less than ten generations after the introduction of *Quercus rubra* to France, introduced populations developed to European land races (DUCOUSSO *et al.* 1997). This shift was accompanied by genetic changes too.

Fagus sylvatica is a climax species while *Quercus robur* is an intermediate-climax species. They are long-lived, wind-pollinated, and with seed dispersed by birds and mammals. They differ in a few ecological characteristics: *Fagus sylvatica* is shade tolerant and able to grow at high altitudes. Another difference is in time of postglacial migration; *Fagus sylvatica* spread much

later (HUNTLEY & BIRKS 1983) and the adaptedness of individual populations may not have reached the same level as in *Quercus robur*. As regards regeneration of the two species, *Fagus sylvatica* is commonly naturally regenerating in the range in which it occurs in Europe whereas *Quercus robur* generally requires support to obtain satisfactory regeneration (see GEBUREK 1998, BONFILS 1998). During historical time silvicultural intervention was much less applied to *Fagus sylvatica* than to *Quercus robur*.

The importance of life history for the among- and within-population variation has been discussed in many papers (cf. BALIUCKAS *et al.* 2000 and lit. cit.). There are few reports on within-population variation in metric traits in *Fagus sylvatica* and *Quercus robur*. In our previous study including three Swedish *Fagus sylvatica* populations we estimated family variances of 9 % for bud flushing during two years' observations (BALIUCKAS *et al.* 1999). The family variances for juvenile height varied between 5.1 and 16.8 % with the highest value at age 2. JENSEN *et al.* (1997) reported a large heritability (= 0.46) for height at age 17 for 37 Dutch open pollinated families of *Quercus robur* studied in Denmark. In contrast, the heritability for breast height diameter was estimated at 0.10. BALIUCKAS (2000) reported large coefficients of additive variation for bud flushing (15.5–60.9 %), autumn leaf colouring (13.1–41.1 %), and height (22.8–42.4 %) in his study of eight Lithuanian *Quercus robur* populations.

There are some reports on among-population differences in *Quercus robur* and *Fagus sylvatica*. The general trend for both species is that bud set varies clinally, even if the populations originate from a comparatively small geographical range (VON WÜHLISCH *et al.* 1995, KLEINSCHMIT 1993, BALIUCKAS 2000). In contrast, bud flushing showed clinal variation only when provenances from a larger area were in-

cluded. SHUTYAEV (1999) delineated zones based on the variation in bud flushing of *Quercus robur* populations. In *Fagus sylvatica* the most expressed cline for bud flushing was observed along longitudes (VON WÜHLISCH *et al.* 1995) whereas latitude was of significance in *Quercus robur* (JENSEN 2000). In our study of three *Fagus sylvatica* populations (BALIUCKAS *et al.* 1999) there was a significant population effect for height during the entire study period, age 2–4, while we did not observe any significant population effect for bud flushing. The usefulness of markers for understanding population differentiation has frequently been discussed (cf. KREMER *et al.* 1997). The paper by KREMER *et al.* (1997) is instructive since it analyses the differentiation in two metric traits, bud flushing and plant height, and compares it with the differentiation in eight allozyme loci in *Quercus petraea*, a species closely related to *Quercus robur*. They reported a much larger among-population variation in the two metric traits than in the allozymes.

The purpose of our study was to estimate genetic parameters for early growth and growth rhythm traits in *Quercus robur* and *Fagus sylvatica* by analysing open-pollinated families from five and three Swedish populations, respectively. The results will be discussed with respect to gene conservation.

MATERIALS AND METHODS

Acorns were collected from 27 to 30 trees in each of five *Quercus robur* populations in southern and central parts of Sweden (see Table 1). Nuts were collected from 28–30 trees in each of three *Fagus sylvatica* populations in southern Sweden (Table 1). The average distance between sampled trees in stands for both species was approximate 30–40 metres. One-year-old oak seedlings were planted at two sites in 1993 (Lugnet

Table 1. Geographical data of the sampled populations.

No	Location	Number of families	N. Latitude	E. Longitude	Altitude m a.s.l.
<i>Quercus robur</i>					
1	Österbybruk	27	60° 12'	17° 52'	25–30
2	Strömsholm	30	59° 32'	16° 17'	10–15
3	Hjo	28	58° 21'	14° 20'	125–150
4	Ingelstad	28	56° 45'	14° 55'	160
5	Rödningeberg	27	55° 34'	13° 51'	35–75
<i>Fagus sylvatica</i>					
1	Hyssna	30	57° 33'	12° 35'	81
2	Ryssberget	28	56° 09'	14° 26'	20–130
3	Marsvinsholm	28	55° 28'	13° 23'	40

59° 40' and Öland 56° 38') with the exception of the most southern population (55° 34') in the Lugnet trial. Beech seedlings of the same age were planted only at the southern site the same year.

A split-plot type of design of the experiment was used with all families of one population kept in a big sub-block, which in turn had six replications of randomised six-tree plots at a spacing of 1 × 1.2 m between trees. A prerequisite from the funding organisation was that the trials should be converted to seedling seed orchards without mixing of populations.

The updating of recordings was done annually during a 3-year period up to age 6. The traits, except for height, were recorded in classes as follows: bud flushing (0–5), leaf autumn colouring (0–4), or leaf fall (0–5), spring frost damage (0–3). The more advanced the stage the higher the recorded class.

Statistical methods

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

The transformations of data used for analysis of variance on family plot mean level were

$$\arcsin \left(\frac{x}{x_{max}} \right) - \text{for traits assessed in classes, where } x$$

= plot mean value, and x_{max} = maximal trait value. The two models used in the analysis of variance were:

$$(1) \quad y_{iklm} = \mu_o + s_i + b_{k(i)} + f_i + (sf)_{il} + \epsilon_{iklm}$$

where s_i – site effect as fixed, $i = 1, 2$, $b_{k(i)}$ – effect of block within site as fixed, $k = 1, \dots, 12$, f_i – family effect, $l = 1, \dots, 30$ (the numbers differ in populations), $(sf)_{il}$ – the effect of interaction between site and family, ϵ_{iklm} – the error term.

$$(2) \quad y_{kl} = \mu_o + b_k + f_l + \epsilon_{kl}$$

where b_k – effect of block, $k = 1, \dots, 6$, f_l – effect of family, $l = 1, \dots, 30$ (the number differ in species/population), ϵ_{kl} – the error term.

Data for the two sites were pooled in model 1, which was applied for *Quercus robur*. Model 2 was applied for analyses of the separate populations in both species.

The following formula was used to calculate additive genetic coefficients of variation:

$$CV_A = \frac{\sqrt{4 \sigma_f^2}}{\bar{x}}$$

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

To estimate the contribution of each family to the interaction variances in each population, the ecovalences of families by populations were calculated on family plot mean level. This type of analysis was done for populations where family × site interaction was significant. The significance of ecovalence values of families was tested using the method developed by SHUKLA (1972).

Genetic correlations were calculated for each population separately according to the formula:

$$r_A = \frac{\sigma_{xy}}{\sqrt{\sigma_x^2 * \sigma_y^2}}$$

where σ_{xy}^2 – covariance between trait x and y , σ_x^2 and σ_y^2 – family variance component for the trait x and y . Correlations were not calculated when the standard error of the family variance component exceeded 60 % of the estimate of the component. Three types of genetic correlations were computed: (1) correlations between the same trait assessed two or more years; (2) correlations between different traits assessed the same or different years; (3) correlations between the same trait assessed at the two different sites. Genetic correlation coefficients were calculated at individual observations level and using procedure AI-REML, software DFREML, "DxMUX" program (MEYER 1997). Block effect was set as fixed.

RESULTS

Owing to the experimental design, only within population genetic variation could be studied. However, mean values for traits assessed are shown in Table 2, which indicates that the differences among populations are minor with the possible exception of bud flushing at age 6 in *Q. robur* and height in *F. sylvatica*.

To illustrate the major trends in family variance components and CV_A in our investigation, Figs. 1–4 were constructed. To get an impression of the precision of the estimates of the family variance components, the percentage of the standard error of the family variance component at each assessment was calculated. The means of these percentages are indicated in Figs. 1–2. The *Q. robur* populations possess large family components in most traits studied with fairly good precision in most cases. Height in the population from latitude 56° 45' and frost damage in populations from latitudes 58° 21' and 59° 32' constitute clear exceptions to this. Generally the precision of the estimates was lower in *F. sylvatica* than in *Q. robur*. Bud flushing in the two

Table 2. Swedish *Quercus robur* (*Qr*) and *Fagus sylvatica* (*Fs*) population mean values (in bold) and their range of family mean values for height and phenological traits at various ages in the Öland field trial. Only one assessment per year is illustrated for phenological traits.

Population	Final height, cm			Bud flushing, stage				Growth cessation, stage		
	Age 3	Age 4	Age 5	Age 3	Age 4	Age 5	Age 6	Age 3	Age 4	Age 5
<i>Qr</i> 60° 12'	43.8	72.0	107.3	1.4	1.8	1.1	2.5	2.1	2.6	2.5
	31.2–53.3	51.8–86.6	83.9–124.7	1.0–2.1	1.4–2.6	0.7–1.6	1.9–3.6	1.8–2.5	1.9–3.4	1.7–3.0
<i>Qr</i> 59° 32'	49.0	85.2	118.3	1.5	2.0	1.1	2.6	1.9	2.9	2.4
	41.5–59	70.5–99.6	98.8–138.5	1.0–2.1	1.3–2.7	0.8–1.6	1.7–3.4	1.7–2.3	2.4–3.7	1.8–3.1
<i>Qr</i> 58° 21'	47.3	84.7	115.4	1.8	2.6	1.4	3.3	1.8	2.6	2.6
	40.6–55.7	75.5–99.8	100.8–131.4	1.2–2.6	2.0–3.3	0.9–1.8	2.6–3.8	1.6–2.1	2.1–3.1	2.2–3.1
<i>Qr</i> 56° 45'	48.0	85.2	116.9	1.7	2.6	1.2	3.3	1.9	2.3	2.1
	38.3–60.7	66.8–104.7	90.4–141.4	1.3–3.2	2.0–3.3	0.8–1.5	2.8–3.9	1.6–2.1	1.7–2.8	1.8–2.3
<i>Qr</i> 55° 34'	43.8	90.0	116.1	1.1	1.3	0.9	2.1	1.6	2.1	1.9
	35.3–53.5	76.1–110.4	95.8–141.2	0.7–1.3	0.7–1.7	0.7–1.2	1.4–2.8	1.1–1.9	1.6–2.8	1.4–2.8
<i>Fs</i> 57° 33'		79.9	102.7	3.8	2.7	1.0	2.3		2.1	3.5
		64.1–94.3	83.6–125.0	3.3–4.5	2.2–3.5	0.8–1.3	1.6–3.3		1.7–2.6	3.1–3.7
<i>Fs</i> 56° 09'	65.5	92.5	127.9	3.9	2.5	1.3	2.6	2.5	2.3	4.0
	59.0–73.7	82.7–106.6	113.7–147.6	3.3–4.4	2.2–2.7	1.0–1.6	1.9–3.3	2.3–2.7	2.0–2.6	3.9–4.0
<i>Fs</i> 55° 28'	79.8	113.2	146.1	3.6	2.2	1.2	2.4	2.5	2.0	3.5
	68.7–88.0	99.8–129.1	124.7–160.1	3.2–4.0	2.0–2.5	1.0–1.5	2.0–3.1	2.2–2.9	1.7–2.6	3.2–3.9

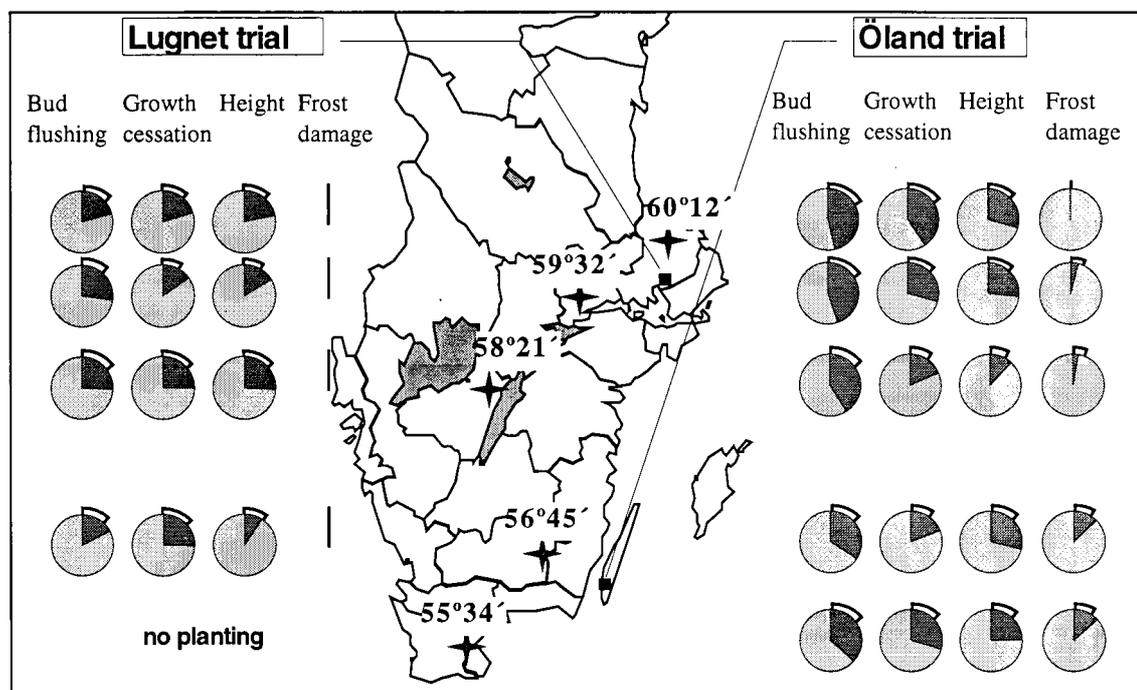


Figure 1. The mean percentage family variance components and mean standard errors (the protuberant part of the pie) of *Quercus robur* populations in two field trials presented at the latitude of the corresponding population. For calculation of the means of the standard errors see text. The means of the family variance components are based on assessments at ages 3–6 with fewer of the assessments at the Lugnet trial.

species proved to be the most heritable and stable trait studied. The average estimations of the family variance components in *Q. robur* populations were higher and

more precise at the southern site (Figure 1). The estimates of the 58° 21' population were among the highest at the northern site while the opposite was the case at

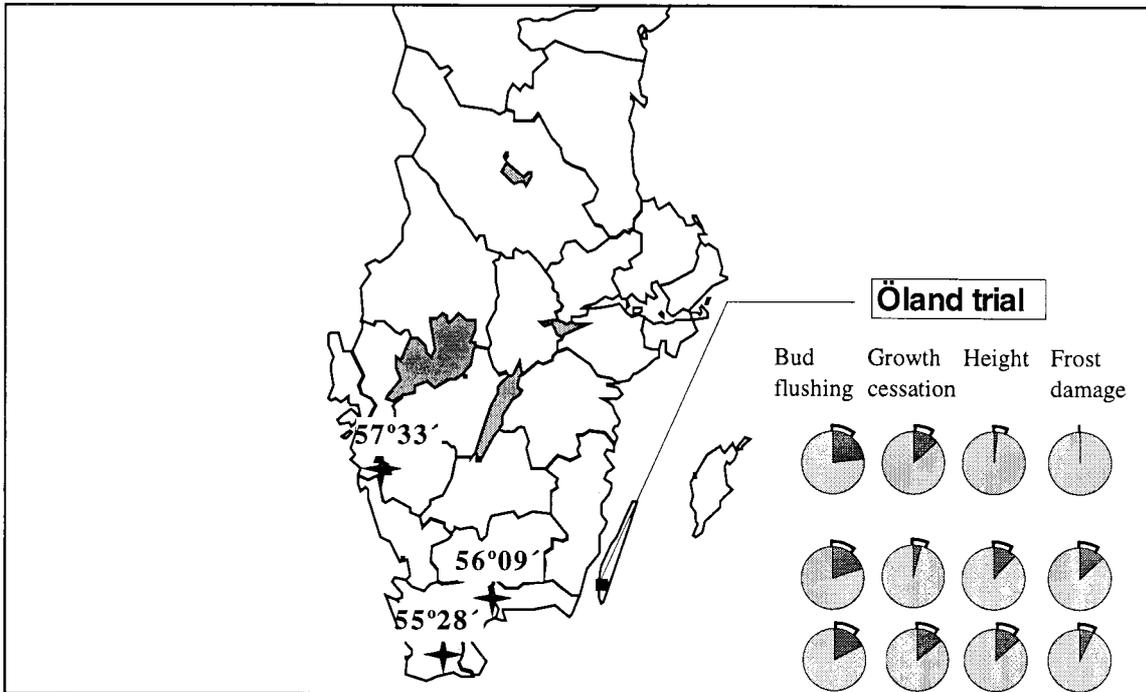


Figure 2. The mean percentage family variance components and mean standard errors (the protuberant part of the pie) of *Fagus sylvatica* populations in two field trials presented at the latitude of the corresponding population. For calculation of the means of the standard errors see text. The means of the family variance components are based on assessments at ages 3–6.

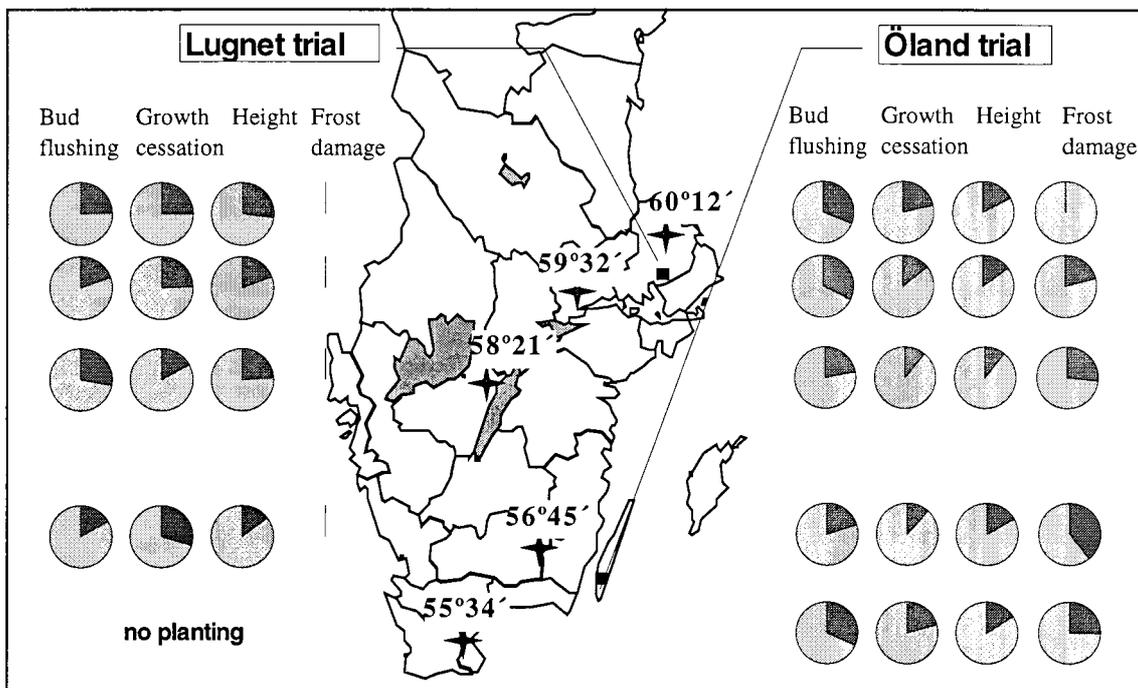


Figure 3. The mean coefficients of additive variation of *Quercus robur* populations in two field trials presented at the latitude of the corresponding population. The means of the CV_A are based on assessments at ages 3–6 with fewer of the assessments at the Lugnet trial.

the southern site, indicating difference in response to environment of traits in the families of this population.

Overall, the ranking of *Q. robur* populations for the traits studied did not differ much between the two sites.

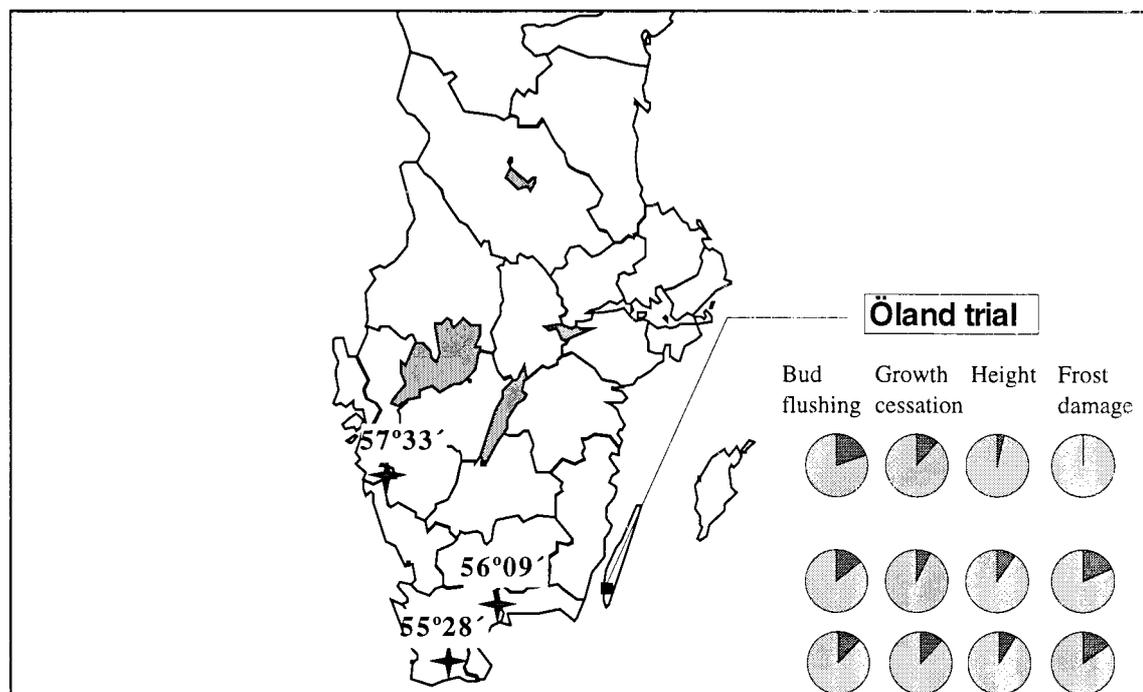


Figure 4. The mean coefficients of additive variation of *Fagus sylvatica* populations in the Öland field trial presented at the latitude of the corresponding population. The means of the CV_A are based on assessments at ages 3–6.

Table 3. Percentage family and family × site interaction variance components ± standard errors and significances of family and family by site interaction effects in *Quercus robur* populations at age 5 for growth rhythm and at age 4 for height. Significance of family × site interaction effect was obtained by ANOVA, model 1 in M & M. Number of families of the total number of families with an ecovalence contributing significantly to the family × site interaction are shown in brackets.

Trait	Source of variation	Populations			
		60° 12'	59° 32'	58° 21'	56° 45'
Bud flushing	Family	20.3 ± 10.0 ***	31.0 ± 10.7 ***	34.5 ± 16.8 ***	21.3 ± 10.4 ***
	Site × family	7.0 ± 6.2	2.1 ± 4.0	12.0 ± 7.7 * (11/16)	2.2 ± 5.8
Autumn leaf colouring	Family	34.2 ± 12.6 ***	15.0 ± 7.4 ***	13.7 ± 12.1 ***	14.7 ± 9.4 ***
	Site × family	0.0	6.2 ± 5.7	20.0 ± 11.5 *** (11/16)	7.6 ± 7.4 *(4/17)
Height	Family	16.4 ± 8.3 ***	7.2 ± 6.3 ***	6.5 ± 9.5 ***	10.6 ± 9.2 **
	Site × family	3.0 ± 5.6	9.2 ± 7.0 * (3/27)	17.0 ± 11.0 ** (7/16)	10.7 ± 8.7 * (2/17)

No clinal trend for any trait could be seen. Variation in spring frost damage was noted for the southern populations at the southern site, whereas there was almost no frost damage at the northern site making it pointless to carry out an ANOVA for this trait at this site.

The mean estimates of the CV_A rarely exceeded 25 % in any of the two species. The mean CV_{AS} were mostly larger in *Q. robur* than in *F. sylvatica* for the same trait (Figures 3 and 4). In agreement with the estimates of family variance components, CV_{AS} in most cases were largest for bud flushing. The large estimates in growth rhythm traits are not necessarily accompanied

by the estimates of the same magnitude for height (Figures 3 and 4).

Only one of the four *Q. robur* populations (58° 21') consistently showed significant family × site interaction (Table 3). This population originates from a slightly more continental climate than the other populations. As seen from Table 3, several families contributed to the interaction according to the estimates of family ecovalence values.

Genetic correlations for bud flushing between years in *Q. robur* populations were strong and stable (Table 4). Bud flushing and leaf colouring gave no correlation,

Table 4. Extreme values of genetic correlation coefficients \pm standard errors of individual populations within and between traits assessed at several assessments at the Öland trial. The ages, at which correlations were obtained, are presented in brackets. The first figure refers to the trait in the row and the second to the trait of the column.

Group of traits	Bud flushing		Leaf colouring		Height	
	min	max	min	max	min	max
<i>Quercus robur</i>						
Bud flushing	0.48 \pm 0.10 (3–6)	0.96 \pm 0.03 (5–6)	–0.32 \pm 0.15 (3)	0.31 \pm 0.13 (3)	–0.72 \pm 0.15 (6–5)	0.82 \pm 0.11 (3)
Leaf colouring			0.46 \pm 0.12 (3–5)	0.84 \pm 0.06 (4–5)	–0.73 \pm 0.11 (4–5)	0.06 \pm 0.08 (4–3)
Height					0.93 \pm 0.03 (3–5)	1.0 \pm 0.01 (4–5)
<i>Fagus sylvatica</i>						
Bud flushing	0.62 \pm 0.11 (4–6)	1.0 \pm 0.07 (5–6)	–0.42 \pm 0.17 (3–5)	0.15 \pm 0.10 (3)	–0.54 \pm 0.12 (3–5)	0.07 \pm 0.14 (6–5)

while the correlation coefficients between bud flushing and height were medium strongly positive at younger age but showing a tendency to disappear or became negative with increasing age as seen from Table 4. The relationship between these two types of trait over age in *F. sylvatica* was opposite with increasing strength of the relationship by age (Table 4).

DISCUSSION

Family variance components and CVA

The CV_A s should normally be more informative about long-term potential for adaptation than the family variance components. However, the CV_A s may be overestimated for phenological traits if the mean value of the trait is extremely low. The mean value is the denominator in the ratio for derivation of CV_A . Only once did an extremely low value, < 1 , for the phenological traits occur in our material (Table 2), which means that the estimates of CV_A are fairly reliable. The relatively high estimates of CV_A for *Q. robur* (Fig. 2) suggest that there are good prospects for adaptation and breeding, especially for bud flushing.

Except for frost damage there is a fairly good precision in the estimates of the family variance components (Fig. 1), with somewhat better precision in the southern Öland trial. At this test site the environmental disturbances were limited during the test period, which probably explains the better precision. The estimates for bud flushing in *Q. robur* show again that this adaptive trait is highly heritable (cf. BALIUCKAS 2000). More-

over, BALIUCKAS (2000) found that bud flushing of half-sib families of *Q. robur* populations in Lithuania at juvenile age was strongly correlated with bud flushing of the mother trees. This indicates that the phenological structure of *Q. robur* populations will be maintained in case of equal probability of regeneration for each phenological class. During the Lithuanian study of *Q. robur* populations (BALIUCKAS 2000) it was noted that different populations produced acorns in different years. If this difference remains there is a possibility that assortative mating occurs, which may give rise to population differentiation if a population fruiting a certain year is characterised by different phenological performance from a population fruiting another year. It was observed that acorns from *Q. robur* mother trees with early flushing are bigger (BALIUCKAS unpublished), so maternal effect on height at early age cannot be excluded. A maternal effect may be traced in the development of the family variance components for height over time. Since there was no trend for reduction of the family components, either in *Q. robur* or *F. sylvatica*, it is less likely that maternal effects were of great significance in our study.

Populations of *F. sylvatica* differed only slightly with respect to bud flushing (Table 2) and even the range of family mean values within the individual populations was less than in *Q. robur*. Compared to our previous study of family variation in *F. sylvatica* (BALIUCKAS *et al.* 1999) the family variance components for bud flushing was larger in the present study while there was a small difference between family variance components for height in the two studies. The

difference observed may be due to difference in weather conditions at the two sites, latitudes 56° 38' and 59° 40', respectively, with a generally more compressed phenology at northern sites. In the presence of a large variation in flushing dates of the families, frost exposure may hit families differently, leading to large among-family variation in height. The absence of frost damage in the northern population of *F. sylvatica* may have influenced the small family component for height in that population (Figure 2). DEMESURE *et al.* (1996) in their study on chloroplast DNA of *F. sylvatica* in Europe concluded that northern populations passed a bottleneck at the time of postglacial recolonization. If this is true it could explain the less pronounced variation in *F. sylvatica*.

Family × site interaction

There was a strong and significant ($p < 0.001$) effect on plant height with approximately 30 % smaller plants at the northern site. As regards the phenological traits, estimates on site effects are not equally straight forward since the number of recordings must be frequent to allow such a comparison. However, the estimates of family × site interaction are not affected by this shortcoming since the interaction is mainly a test of rank change of the families between the two sites. As expected, the family × site interaction for height was usually strongest among the traits studied. The reason for this expectation is that height is a cumulative trait and the existing differences tend to increase with age, if they exist. Thus, the number of growth cycles was not correlated with bud flushing and only weakly positively correlated with height at age 2 in the experiment with Lithuanian *Q. robur* populations (BALIUCKAS unpublished data). The number of seedlings that had a third growth cycle comprised 5.8 % of the total number of seedlings with a population range of 2.8–8.5 %. STEINER and KREMER (1997) found that growth cycles differ within a tree of *Q. rubra* over years at juvenile age and that *polycyclism appeared to account for much of the plasticity in growth habit*.

As seen from Table 3 the family × site interaction variance components were larger for the two southern populations than for the corresponding components of the two northern populations with one exception. Thus, there was no significant family × site interaction for bud flushing in the southernmost population in spite of its large difference in mean values at the two sites. The southern origin and thereby poorer adaptedness at the northern test site may be one reason for the difference in importance of the family × site interaction between the southern and northern populations. It was noted that the bud flushing started earlier and that leaf colouring

distribution in family mean values of the southern populations was more compressed (no data presented here).

Genetic correlations

The strong correlations between the same trait studied in different years both in *Q. robur* and *F. sylvatica* was expected since it has been shown in many reports that phenological traits are strongly correlated in other tree species (*eg.* EKBERG *et al.* 1994). The strong correlations between bud flushing in different years in *F. sylvatica* agree with the data presented by VON WÜEHLISCH *et al.* (1995). This means that phenological observations can be carried out during one season to get satisfactory results.

The genetic correlation coefficients between leaf colouring in different years in *Q. robur* were more or less of the same magnitude as the corresponding ones for bud flushing. Despite the absence of any correlation between these two traits, the ranking within each one was almost stable and it is evident that it is not possible to predict the duration of growing season of a family at juvenile age by use of bud flushing dates or growth cessation dates only. Data from *Pseudotsuga menziesii* (LI & ADAMS 1993) and data from Lithuanian *Q. robur* show that bud flushing and growth cessation correlations increase considerably with age, which means that the observations at juvenile age may not be long-lasting. The correlations between leaf colouring and height in *Q. robur* were mostly negative, in agreement with many other studies of tree species (*eg.* VELLING 1979). It is possible that frost damage contributed to the stronger negative relationship at higher age between leaf colouring and height. According to VIA and LANDE (1985) the negative genetic correlations between traits within the site may reduce the possible number of environments to which a plastic response may have evolved. Bud flushing and leaf colouring genetic correlations in *F. sylvatica* populations serve as an illustration of this.

Implications for gene conservation

Among ecologists fears were raised that many tree species would not be able to migrate fast enough to cope with the expected global warming caused by greenhouse gases (*eg.* DAVIES 1988). The other means to cope with global warming, adaptation, has frequently been neglected among ecologists (*cf.* ERIKSSON 1999). ERIKSSON (1999 and 2000) strongly emphasised the need for additive variance in populations in the event of global warming.

It is of significance that there were large coefficients

of additive variation and family variance components in both species (Figs. 1–4). In conclusion our populations have the potential for adaptation under changed environmental conditions. In this connection it is of interest to note that so called after-effects (cf. SKRØPPA & JOHNSEN 2000) were observed in *F. sylvatica* by MADSEN (1995). He observed difference in bud flushing related to the temperature conditions during the year of maturation of the nuts. If this phenomenon is confirmed, it means that a rapid adaptation to the new environmental conditions may take place in the event of global warming.

Swedish forest sites have a mosaic pattern, which may favor the process of interspecific hybridization (cf. RUSHTON 1978). Moreover, it is assumed that interspecific hybridisation is of greater significance for *Q. petraea* and that it is most frequent in marginal areas (DUPOUEY & BADEAU 1993). If interspecific hybridization occurs it causes an increase of the additive variance of the recipient population at the cost of adaptedness in the progeny. However, GREGORIUS (1996) stated that intraspecific adaptation is preferable to interspecific adaptation for ecosystem stabilisation. KLEINSCHMIT and KLEINSCHMIT (2000) claimed that it is likely that *Q. petraea* will become selectively more competitive than *Q. robur* under altering climate conditions.

Since this investigation was not designed to study population differentiation we cannot discuss sampling of gene resource populations at any depth. However, the Öland experimental site is very homogeneous. With this in mind it is striking that the differences in population means of the *Q. robur* populations are so small, suggesting that selection of any of these populations would satisfy the demand for sampling of gene resource populations. However, our results do not agree with the large among-population differentiation of Lithuanian *Q. robur* populations (BALIUCKAS 2000). A large among-population variation was also observed by VAKKARI (2000) in his isozyme study of marginal Finnish *Q. robur* populations. The history of these populations is of importance for a solid interpretation of such a result but it may be speculated that genetic drift has occurred in the small isolated populations. Such an explanation hardly holds for the large genetic diversity of adjacent German populations of *Q. robur* and *Q. petraea* reported by MAURER *et al.* (2000). HERZOG (1996) recommended numerous and sufficiently large *Q. robur* stands for *in situ* maintenance owing to results obtained from isozyme studies. Owing to the German impact on Baltic countries during the 19th century it would be tempting to attribute part of the large variation among Lithuanian *Q. robur* populations to the existence of two types of populations, German and indigenous Lithuanian populations (BALIUCKAS 2000). However, the

Lithuanian populations included in that investigation were selected to be indigenous. Based on the results from other studies presented above it would be unwise to recommend only one *Q. robur* population for gene conservation of this species.

The larger among-population variation observed for juvenile height in *F. sylvatica* (Table 2) suggest that it would be useful to include several populations in the gene conservation of this species.

CONCLUSIONS

The substantial additive variance in most populations for height and phenological traits is promising for a continued adaptation in these two species. This means that *in situ* nomination of stands of these species would be an inexpensive option for their gene conservation. A prerequisite is that regeneration is guaranteed in the gene resource populations (cf. PLIURA & ERIKSSON 1997). For both species gene resource populations nominated in this way could advantageously be integrated with European networks of these species. The observed variation also indicates that improvement could easily be obtained in breeding programmes. The strong correlations between phenological traits in different years mean that for breeding purposes it would be satisfactory to carry out phenological observations one year only.

ACKNOWLEDGEMENTS

We are grateful to Drs INGER EKBERG and ALFAS PLIURA for valuable comments and also to HARTMUT WEICHEL for precise recordings of data. We are grateful to Dr DAVID CLAPHAM for revision of the English. The scholarship from The Royal Academy for Forestry and Agriculture for VIRGI LIJUS BALIUCKAS for supporting studies in Sweden is much appreciated. This project was made available by a grant from Swedish Farmers' Foundation for Agricultural Research, which is gratefully acknowledged.

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