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Life History Traits and Broadleaved Tree Genetics

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SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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Most broadleaved tree species play a minor role in Scandinavian and Baltic forestry, therefore little information on metric trait variation exists so far. The Forestry Convention signed by many European countries requires that gene conservation programs have to be developed for broadleaved tree species. Studies of within- and among-population genetic variation are of great importance for gene conservation strategy and the design of gene conservation and long-term breeding programmes.

Our hypothesis is that life history traits influence the among- and within-population genetic variation. Three experiments, with different sets of species included in each, were conducted in Sweden. We have selected populations of *Quercus robur*, *Fagus sylvatica*, *Fraxinus excelsior*, *Acer platanoides*, *Prunus avium*, *Prunus padus*, *Sorbus aucuparia* and *Alnus glutinosa* from across their range of distribution in Sweden. A complementary study of progenies of Lithuanian *Quercus robur* populations was done in a Lithuanian experiment. Open pollinated families were studied in all experiments, covering ages 2-6. Except for bud flushing, there was no clear evidence for increased within-population variation for climax compared to pioneer species in the traits studied. Substantial gene flow may occur even in intermediate and insect pollinated species. The largest within-population variation estimates, regardless of species, occurred for bud flushing.

A strong parent-offspring relationship was revealed for bud flushing in *Quercus robur*, which indicates the presence of assortative mating in the populations. In addition, strong and stable genetic correlations across years in all species suggest high juvenile-mature correlations for this trait. The genetic parameters of populations from our experiments showed that northern and southern populations are equally good for gene conservation purposes.

Key words: adaptive traits, gene conservation, genetic variation, juvenile age, open pollinated families, populations.

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Abstract

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Except for bud flushing, there was no clear evidence for increased within-population variation for climax compared to pioneer species in the traits studied. Substantial gene flow may occur even in intermediate and insect pollinated species. The largest within-population variation estimates, regardless of species, occurred for bud flushing.

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Key words: adaptive traits, gene conservation, genetic variation, juvenile age, open pollinated families, populations.

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Appendix

Papers I-V

This thesis is based on the following papers, which are referred to in the text by their corresponding Roman numerals.

I. Baliuckas, V., Ekberg, I., Eriksson, G. & Norell, L. 1999. Genetic variation among and within populations of four Swedish hardwood species assessed in a nursery trial. *Silvae Genetica* 48: 17–25.

II. Baliuckas, V., Lagerström, T. and Eriksson, G. 2000: Within-population variation in juvenile growth rhythm and growth in *Fraxinus excelsior* L. and *Prunus avium* L. *Forest Genetics* 7 (3): 183-191.

III. Baliuckas, V., Lagerström, T. & Eriksson, G. 2001. Within-population variation in juvenile growth rhythm and growth in *Quercus robur* L. and *Fagus sylvatica* L. *Forest Genetics* 8 (4): 259–269.

IV. Baliuckas, V. & Pliura, A. Genetic variation and phenotypic plasticity of *Quercus robur* L. populations and open pollinated families in Lithuania. (Submitted to *Scandinavian Journal of Forest Research*).

V. Baliuckas, V., Lagerström, T. & Norell, L. Genetic variation among and within populations in Swedish species of *Sorbus aucuparia* L. and *Prunus padus* L. assessed in a nursery trial. (Manuscript).

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Introduction

Gene conservation

The prime objective in gene conservation is to safeguard the potential of population for adaptation (see Eriksson 2001). Allelic effects and frequencies jointly generate genetic variation. Alleles at medium frequencies contribute most to the additive variance in populations, so they will respond most strongly to natural selection. Studies of adaptive traits as well as of numerous 'neutral' molecular markers have shown that most genetic variation in temperate and boreal forest tree species exists within populations (e.g. Jensen et al. 1997, Kremer et al. 1991). It is therefore very important in gene conservation to select populations, which are likely to be able to adapt to any alteration of the environment. In marginal environments among-population genetic variation may be more important as a result of random events and a certain degree of specific adaptation that was "reached" by direct natural selection. Steep environmental gradients are reflected in large population differentiation in adaptive traits among populations (e.g. Hurme et al. 1997).

Uncertainty about the rate of climate change and about the future use of forest resources calls for dynamic gene conservation (e.g. Eriksson et al. 1993, Finkelday & Hattemer 1993). The *in situ* gene conservation method of MPBS (multiple population breeding system), developed by Namkoong (1984), could be successfully applied to commonly occurring noble hardwood species (Eriksson 2001). This system can be used jointly with a long-term tree breeding programme. Some associated species may benefit from gene conservation of keystone species (cf. Varela & Eriksson 1995). Robustness of genetic structure here defined as among- and within-population variation of a species, of most temperate and boreal tree species prove that there is no need to concentrate the efforts of gene conservationists on preserving individual multilocus genotypes, but rather to create good prospects for efficient generation of new combinations via maintaining dynamic processes in gene resource populations (see Savolainen 2000).

Relatively more populations of pioneer species are needed for gene conservation and/or breeding populations compared to climax ones. Similarly, a smaller number of populations have to be selected for gene conservation in species with large gene flow than in species with restricted extensive gene flow (Graudal et al. 2001). Classification of species by their abundance would be useful in practical gene conservation (Eriksson 2001). Until now the potential to identify populations for gene conservation using molecular markers methods has been limited (Mariette et al. 2001). The adoption of gene conservation strategies for various broadleaved tree species calls for more comparative studies of species with different life history traits, as was emphasised by the EUFORGEN network. There is a need to detect the differences in species genetic structures in adaptive traits. The criteria for population selection in separate species should ensure the sufficient within-population genetic variation in adaptive traits as ones of prime importance for successful population development in coming generations.

Climate change and adaptation

Among the main abiotic factors that cause alteration of species' distribution range, the changes in climatic regime can be rapid compared to eustatic events and tectonic processes (see Futuyma 1998). There are three means by which a species copes with changes in the environment: genetic response, physiological response, and migration. However, there is a belief among ecologists that migration will not be fast enough to cope with the predicted change (e.g. Davies 1988). Because of differences in ability of species to react genetically to possible changes, knowledge of the limits of tolerance and of those adaptive traits thought to be influenced by climatic conditions are of prime importance. Different response to photoperiod as a consequence of intensified adaptation processes may be observed for northern compared with southern populations since photoperiodic variation increases with latitude. A difference in response to ozone of southern compared to northern *Fagus sylvatica* populations in Europe has also been observed (Paludan-Müller et al. 1999). A simulation of climatic warming in *Acer saccharum* populations showed more evidence for physiological acclimation than of ecotypic differentiation (Gunderson et al. 2000).

Although global warming would presumably first affect southern, low elevation and continental peripheries of forest tree species' natural ranges, target populations for gene conservation, especially at the margins of a range, should be characterised by high phenotypic plasticity, which is here defined as the amplitude for a trait of a genotype studied in at least two different environmental conditions (cf. Bradshaw 1965). This is important since the ability of trees to respond to climatic change by selection, and especially by migration, is quite limited. The typical and at the same time variable sites facilitate promotion of adaptive processes and could guarantee long sustainability under perspectives of rapid climate change. This could be of great importance in regions characterised by interspecific introgression. There are many predictions that the northern limit of tree species will be pushed northwards following global warming, e.g. for *Fagus sylvatica* and *Quercus robur* by Sykes et al. (1996).

In addition to evolutionary factors such as mutation, genetic drift, natural selection, gene flow, and phenotypic plasticity, reproductive environment could be considered a factor increasing adaptedness of species, especially under marginal conditions (Skrøppa & Johnsen 2000). Similarly, Madsen (1995) reported that environmental conditions in the mast year in *F. sylvatica* stands influenced bud flushing dates of offspring.

The chilling requirement in birch populations is highest in maritime populations and lowest in the most continental ones (Leinonen 1996). This is of importance under global warming when populations from maritime climates could be advantageous for cultivation at other localities as well. Some results suggest that populations of pioneer species from the optimal growing conditions are able to adapt better to a broad spectrum of site conditions than those from the margins (Hill et al. 1998). Marginal environments by their nature often are more heterogeneous than those situated centrally, so spatial isolation could be a decisive factor in creation of widely adapted breeding populations for marginal environments (Hill et al. 1998).

Even if hardwoods species have not reached the optimal fitness in their distribution range, results from numerous provenance trials prove that some adaptedness has been reached. The growth rates of continental provenances of *Betula pendula, Quercus petraea* and *Alnus glutinosa* (grown in Britain) were inferior to those of British populations in 90% of the cases, demonstrating the adaptedness of local British populations (Worrell 1992). Continental populations of these species also exhibited inferior survival. Several reports confirm that growth of *Betula pendula* and *B. pubescens* of northern origin is inferior in southern localities to that of local populations (see Jonsson & Eriksson 1986 for a summary). Provenance trials are useful for testing existing adaptedness of local populations. However, often conditions in field trials or forest plantations are not good imitations of the conditions in a natural forest environment.

Migration, geographic distribution and human impact

Information on postglacial migration routes is important for understanding of the current genetic structure of populations. Observed geographic patterns of gene diversity and allelic richness were formed during postglacial migration in many forest tree species (e.g. Comps et al. 2001). The size of the refugia, the routes by which the populations reinvaded and the size of the founder populations have all influenced the gene pool of local populations. In general, the present pattern of species distribution, with continuously extended area and separated islands along marginal area suggests that species migrated not as a single population but along several paths from marginal founder populations. It is assumed that there is a large variation between marginal populations. Between-population variation could play more important role than within-population in migration of species northwards after the glaciation and at present global warming. The great heterogeneity of environmental conditions and variable strong selection have resulted in direct adaptation (Tigerstedt 1994). *Fagus sylvatica* and *Alnus glutinosa* have colonized Central and Northern Europe after the last glaciation from a refugium in the Carpathian Mountains mainly (King & Ferris 1998). Oak species in Europe migrated from three main refugia (Dumolin-Lapegue et al. 1997). *Fraxinus excelsior* migrated mainly from two refugia (Huntley & Birks 1983). However, it is often not possible to detect how many species of the same genus were present in a particular refugium, before they started to migrate northwards. *Alnus glutinosa* was among the first species to reach the present limits of its natural distribution while *Fagus sylvatica* was the last one. Various periods in Holocene caused a decrease in some species and increase in others and the climate dynamics and competitive relationships between species were the main factors causing or influencing species dynamics (Tinner & Lotter 2001).

Oaks are recognized as keystone species in European forest ecosystems and their post-glacial recolonization routes and genetic diversity pattern may partly imply the distribution of diversity in other plant species typical to oak forest tree communities (Kremer 2002). At the same time, the recolonization dynamics can serve as an indication of the possible migration of species under global warming. The various European broadleaved tree species have different domestication histories. Human impact on species occurs through population transfer, regeneration, and the silvicultural regimes applied, and the impact is large as it lasts for centuries. The effort put in by man depends much on the economic importance of the species. Some species, for instance *Alnus incana*, were treated as a 'weed' and extensively removed from forests.

Variation among populations

Pioneer or intermediate hardwood species exhibit more pronounced inter-population differentiation compared with climax species to which they share other life history traits (Hamrick & Godt 1989). Heuertz et al. (2001) reported that among-population differentiation is higher in *Fraxinus excelsior* than has been observed in oak and beech species. A high genetic differentiation was found in Finnish *Acer platanoides* populations (Rusanen et al. 2000). These observations are of crucial importance for sampling strategies for genetic resource conservation and could also be indicative for long-term breeding strategies.

Large population differentiation with respect to isozymes was observed in Finnish marginal populations of *Ulmus laevis* (Mattila & Vakkari 1997). But often patterns of allozyme variation are not correlated with variation in metric traits. This was the case in a Finnish *Pinus sylvestris* study (Karhu et al. 1996). Low among-population differentiation was revealed by aid of molecular markers, although the difference in budset between southern and northern populations was 21 days (Karhu et al. 1996). Molecular markers may therefore be poor predictors of the population differentiation in quantitative traits in other species as well. The extensive gene flow in forest trees maintains selectively neutral allelic uniformity and differentiates loci of adaptive traits.

Geographic pattern of variation

A species with a distribution covering several climatic zones is very likely to show large differences among distant populations. In particular, we expect genetic differentiation along a north-south gradient. It is thought that natural selection is responsible for clinal variation in photoperiodic response, as was demonstrated for several tree species by Håbjørg (1978). Long latitudinal transfer results in poor growth of southernmost populations in northern sites, as they do not build up hardiness prior to autumn frost. Conversely early growth cessation following a long-distance southward transfer was reported by Sylvén as early as during the fourties (Sylvén 1940). This observation has been reported repeatedly (e.g. Clapham et al. 2001). The best domestic fitness in the sense of Skrøppa (1994) is obtained when growth cessation takes place early enough to avoid early autumn frosts but without growth cessation occurring too early. A good example of such a trade off between growth and growth cessation was reported for *Betula pendula* by Velling (1979).

Clinal and ecotypic patterns may exist side by side in some hardwoods species such as *Quercus robur*, *Fagus sylvatica*, *Fraxinus excelsior* (Kleinschmit 1993). Geographical pattern variation of various traits was found in studies of American ash species (e.g. see Clausen 1984, Roberds et al. 1990, Schuler 1994). Some traits demonstrate a clinal pattern while others show an ecotypic one. Growth traits show more ecotypic pattern than growth rhythm traits (Kleinschmit 1993), and this may be partly attributed to founder population effects. Clinal variation is more pronounced in boreal forests. Budset usually reveals a clearer clinal variation pattern than bud flushing (Kleinschmit 1993). It has been demonstrated in *Alnus sinuata* and *Betula papyrifera* that photosynthetic rate has a clinal pattern (Benowicz et al. 2000). A study of *Acer rubrum* open pollinated progeny showed that photosynthetic potential is associated with ecotypic differentiation (Anella & Whitlow 2000).

Performance of some quantitative traits, such as branchiness, branch thickness and wood density in hardwoods is in general not sensitive to transfer southward or northward. This suggests that they do not play as important a role in the processes of adaptation. The ability of species to adapt with respect to an important and highly predictable climatic character such as photoperiod should be considered in gene conservation or breeding programmes.

Variation within population

Limited information about adaptive variation is available, especially in economically less important species. The proportion of within-population to among-population variation is usually higher in wind-pollinated species. This was revealed in the study of growth, phenology and frost resistance in *Quercus robur* open pollinated progeny (Jensen et al. 1997). In a comparison of adjacent populations of *Acer platanoides* and *Betula pendula* large coefficients of additive variation (CV_A) were observed for juvenile growth and phenology traits in *Acer platanoides* (Eriksson et al. submitted). Similarly, there were high estimates of CV_A in a growth chamber experiment in the same study. In addition, gene flow in the two species was estimated at 2.3 and 7.6 for *Acer platanoides* and *Betula pendula* respectively.

Up to three times higher within-population variation than among-population variation was revealed using enzyme markers in *Quercus robur* and *Fagus sylvatica* (Gehle 1999). Strong gene flow under random mating leads to large within-population variation with time unless natural selection is extremely strong (Eriksson 1997).

Life history traits and genetic structure

It is hypothesised that life history traits influence genetic structure. Population structure and ratio of within- to among-population variation are probably influenced by life history traits. Thus, the distribution of genetic diversity at species level as estimated by the aid of isozymes is also dependent on these traits and can explain a quarter of total variation (Hamrick and Godt 1989).

The proportion of among to within-population genetic variation of different species is expected to depend upon mating system (e.g. wind vs. insect pollination), distribution (e.g. wide vs. scattered) and stage in the ecosystem (e.g. pioneer vs. climax). The past interaction of evolutionary factors - natural selection, gene flow, genetic drift, inbreeding, and mutation - is responsible for the existing genetic structure of a species. In species with large random-mating populations the effect of mutations and genetic drift is negligible. In such species the balance between the counteracting factors of natural selection and gene flow is decisive for the genetic structure. If gene flow is considerable it will be a constraint to among-population differentiation and vice versa; if it is limited there is room for differentiation among populations.

The expectation that gene flow in wind-pollinated species is larger than in species with other pollen vectors has been to some extent verified (Hamrick et al. 1992). Tree species maintained more variation within species and within populations than species with other life forms, but had less variation among populations. Woody species with large geographic ranges, outcrossing breeding systems and wind or animal-mediated seed dispersal had more genetic diversity within species and populations, but less variation among populations than woody species with other combinations of traits (Hamrick et al. 1992). Pollen/seed dispersal ratio in oak species is one of the largest compared to other broadleaved tree genera. The number of migrating genes estimated per generation (by pollen and seeds) is about 10 in *Quercus robur* (Zanetto et al. 1994, Kremer et al. 1991). This leads to a large mating neighbourhood area, which was estimated at 12 hectares for *Quercus robur* (Kremer & Menozzi 2001). Somewhat lower figures would be expected for species regarded as intermediate in the succession within an ecosystem. This was confirmed for *Fraxinus excelsior*, for which the mating neighbourhood area was estimated at less than 1 hectare (Heuertz et al. 2001).

Most hardwoods are monoecious, but some, as *Fraxinus excelsior*, are dioecious having female and male gametes located on different trees. The mating system can be regarded as a compromise between evolutionary history, evolutionary potential and the requirements of the present environment (Stern & Roche 1974). Selfing rates in a number of hardwood species do not exceed 5% (e.g. Kremer & Menozzi 2000, Heuertz et al. 2001). Flowering periods in populations of species vary from one to several weeks and this greatly influences the formation of spatial genetic structure, since this trait is heritable and regulated by small numbers of loci (Frewen et al. 2000).

In small populations, genetic drift may be of significance and as a consequence species with small and scattered populations may be characterised by a considerable but non-adaptive among-population differentiation. The extremely large among-population differentiation for isozymes in Finnish populations of *Acer platanoides*, and particularly *Ulmus laevis*, referred to above is a confirmation of this expectation (Rusanen et al. 2000, Mattila & Vakkari 1997).

Evolutionary factors are probably of different strengths in marginal compared to central populations. If this is the case it will have significant implications for the level of among and within-population variation of adaptive traits.

Mast year periods vary not only among species, but can also vary in populations of the same species from distant regions of natural distribution. The period between abundant crop years in broadleaved tree species varies from 2 to 5 years. Pioneer species usually produce many more seeds per tree, creating the possibility for species to invade large areas in one generation. Length of reproductive age and a long-lasting ability to reproduce vegetatively help species to maintain their genetic structure unchanged after founder population establishment, unless human activity is intensive.

Hybridisation and introgression zone formation is species specific and influences the pattern of genetic diversity. It is probable that these processes are more intense in marginal populations. In practical gene conservation it is recommended to select populations where hybridisation is present when the objective is to promote adaptation (Collin 2001).

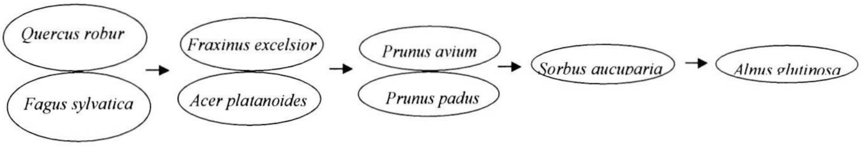
Climax species are expected to be much more specialised than pioneer species (Levins 1963). Sometimes separate species from the same genus can be recognized as pioneer or climax species (Rameau 1990).

Genetic information on hardwoods is quite scarce, so we have to base our assumptions on essential life history traits. Some life history traits believed to influence the genetic parameters of a species are presented in Table 1.

Table 1. Life history traits of some broadleaved species

Species	Stage in ecosystem	Pollen vector	Distribution of populations	Seed dispersal	Life form
Quercus robur	Climax	Wind	Wide continuous	Animals	Long-lived
Fagus sylvatica	„	„	„	„	„
Fraxinus excelsior	intermediate	„	wide scattered	wind-animals	„
Acer platanoides	„	insect	„	„	„
Prunus avium	„	„	scattered	birds	short-lived
Prunus padus	„	„	„	„	„
Sorbus aucuparia	„	„	wide scattered	„	„
Alnus glutinosa	pioneer	wind	„	wind	medium

Species in our study would express within-population variation in decreasing order based on theoretical predictions:



Objectives

The main objective of the study was to estimate genetic parameters of broadleaved tree species with different combinations of life history traits. An objective of the study was also to study the pattern of variation for climatic adaptation within and between populations. To answer these questions, the growth and growth rhythm traits in open pollinated families of several broadleaved species during the juvenile phase were investigated. The data generated may be used for decisions in gene conservation.

Material and methods

Plant materials

Eight broadleaved species were included in this study. Open pollinated families of Swedish and Lithuanian (only *Quercus robur*) native populations were collected and studied in common garden and field trial experiments (Fig. 1). Trees possessing superior phenotype were selected for seed collection, keeping a distance of approximate 30-50 metres between them in order to decrease the probability of genetic identity. This means that in some species such as *Acer platanoides*, *Prunus padus*, and *Sorbus aucuparia* the number of female trees per stand was low.

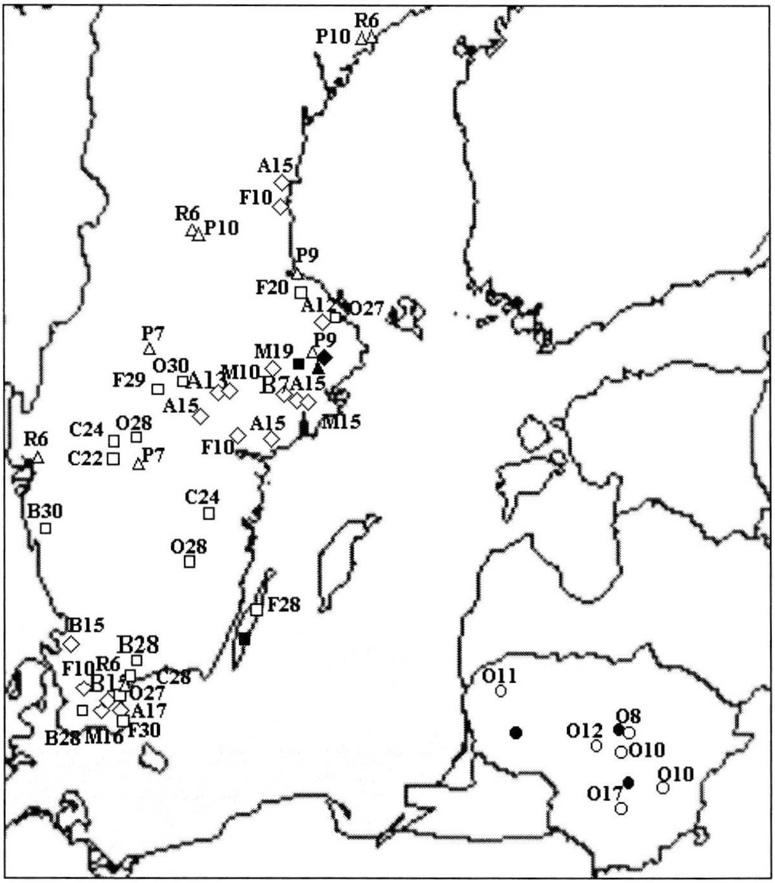


Fig. 1. The illustration of population origins in Sweden and Lithuania. Different symbols denote different series of experiments and the shaded symbols show experiment sites. The letters indicate species (B – *Fagus sylvatica*, A – *Alnus glutinosa*, F – *Fraxinus excelsior*, M – *Acer platanoides*, O – *Quercus robur*, C – *Prunus avium*, R – *Sorbus aucuparia*, P – *Prunus padus*) and numbers show the number of trees sampled.

Registration scales

Our efforts were concentrated most on assessments of growth rhythm and height dynamics traits. Some assessments of growth rhythm traits were performed twice or even three times per season to be able to catch the largest resolution between populations and families.

All traits except for height, leader length, and diameter (recorded in *P. avium* only), were recorded in classes, assuming linear scales. These traits were: bud flushing (0-5), leaf autumn colouring (0-4), or leaf fall (0-5). The recordings, made by experiment (see Table 2), were the following: 1) budset-reflush (0-8), mildew infection in *A. platanoides* (0-2), spring frost damage in *F. excelsior* (0–3), crown form in *A. platanoides* (0-5); 2) spring frost damage (0–3), autumn frost damage (0-3); 3) plant health/conditional status (0-2), flowering abundance (0-3), stage of flower development (0-3), growth after the repeated flush (0-2); 4) spring frost damage (0-2).

The higher the figure the more advanced the stage of trait progress, with the exception of plant status where the highest number indicates the poorest performing plant.

Table 2. Information on the experiments conducted during the study

No. of exp.	*Species*	Number of populations and half-sib families in each	Experimental design	The aim of investigation, the age of plants and number of test sites (paper No)
1	*Alnus glutinosa, Acer platanoides, Fagus sylvatica, Fraxinus excelsior*	3-7 Swedish populations and 7-19 families	Randomised complete block design in 6 or 8 replicates with single-tree plots	Among- and within-population variation at age 2-5 at one experimental site (paper I)
2	*Fraxinus excelsior, Prunus avium, Fagus sylvatica, Quercus robur*	3-5 Swedish populations and 20-30 families	A split-plot experimental design, one population kept in a big sub-block with six replications of randomised six-tree plots per family (design enables conversion to SSO)	Within-population variation at age 3-6 at two experimental sites (paper II & III)
3	*Prunus padus, Sorbus aucuparia*	4-6 Swedish populations and 6-10 families	A split-plot experimental design, one population kept in a separate block with six replications of randomised four-tree plots per family (design enables conversion to SSO)	Among- and within-population variation at age 2-6 at one experimental site (paper V)
4	*Quercus robur*	12 Lithuanian populations in the nursery and 6 in field trials with family number 6-17	An incomplete randomised block design with 8-tree row-plot in the nursery. Randomised complete block design in 4 replicates with single-tree plots in field trials	Among- and within-population variation and parent-offspring relationship at age 2-4 at one and at age 6 at 3 test sites (paper IV)

Statistical analysis

The genetic parameters for genotype by environment (GxE) interaction in each species (papers II, III & IV) were estimated for a single trait using mixed model equations (MME) and the restricted maximum likelihood (REML) method (SAS Institute Inc. SAS/STAT® software.). Family plot mean data were used in the calculations of genetic parameters in the papers I, II & III, while individual observations were used in papers IV & V. Where necessary to obtain homoscedasticity for the residuals, data were transformed by arcsine or square root for traits registered in classes, and logarithmic transformation for metric traits (papers I, II, III). Additive genetic coefficients of variation were calculated in all except paper I. The analyses of variance were done with PROC GLM, Type III SS. The significance of ecovalence values of families was tested using the method developed by Shukla (1972) in analysis of genotypic stability.

Genetic correlation coefficients were calculated at the individual level using the AI-REML procedure of DFREML software (Meyer 1997). Various types of genetic correlations were computed for separate populations (papers II, III, IV) or pooled data (paper V): 1) correlations between the same trait assessed two or more years; 2) correlations between different traits assessed in the same or different years; 3) correlations between the same trait assessed at the two different sites. In calculating the second type of correlation, assessments of the same trait in different years were considered as traits x and y. Correlations were calculated only when the standard error of the family variance component was less than 60 % of the estimate of the component.

MAIN RESULTS

Within-population genetic variation

To illustrate some of the results obtained in this study observations of bud flushing for two populations from each species are shown in Fig 2. The populations were selected according to extreme estimates of family variance components. In most cases even the population with the lowest variance component showed a variation among the families studied. The most conspicuous difference was noted for the *Quercus robur* population Kulupenai, in the Lithuanian nursery study (paper IV). The relatively small standard errors are noteworthy. The largest standard errors were noted for *Alnus glutinosa*.

In the study of *Acer platanoides*, *Alnus glutinosa*, *Fagus sylvatica* and *Fraxinus excelsior* (paper I) the largest family variance components were noted for bud flushing with estimates larger than 10% of the total variance, the largest being observed for *Acer platanoides* and *Fraxinus excelsior*. The estimates slightly decreased over years, but remained highly significant. The family components for growth cessation were usually less than 5% of the total variance (no recordings were obtained for *Fagus sylvatica*) and did not show large differences between the species. Similar estimates for height were mainly of the order of 3-10% and showed a slight decrease with age. *Fagus sylvatica* had the largest value. Among the populations of *Acer platanoides*, the northern one showed the largest estimates for all traits studied (bud flushing, growth cessation and height).

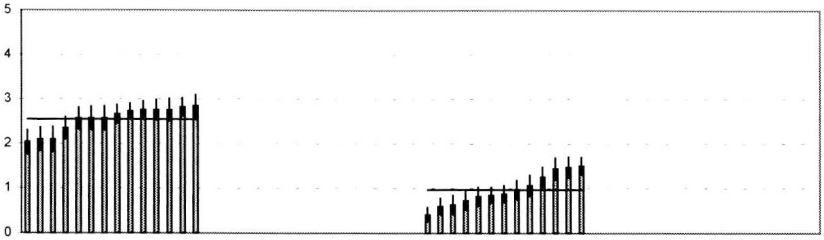
The studies of *Fraxinus excelsior* and *Prunus avium* (paper II) revealed high genetic variation within the populations witch had a small tendency to decrease with age. The parameters obtained were of the same magnitude in both species, but *Fraxinus excelsior* unlike *Prunus avium*, showed larger family variance components and CV_As in northern than in southern trials. Family component for growth cessation were high, but somewhat smaller in *Fraxinus excelsior* than in *Prunus avium*, and also smaller than for bud flushing in either species. For height the family variance component was of the same order as for bud flushing, decreasing slightly in *Fraxinus excelsior* with age. In contrast with family variance components, CV_As were generally higher in *Fraxinus excelsior* than in *Prunus avium* in the traits studied, except for autumn frost damage. Notably, northern populations of *Fraxinus excelsior* had higher estimates of family variance components and CV_As for bud flushing and height than southern ones. The estimates obtained for *Fraxinus excelsior* were greater for bud flushing and height at the northern site than the southern site.

In the Swedish population study of *Quercus robur* and *Fagus sylvatica* (paper III) it was observed that the highest estimates of family variance components as well as CV_A were obtained for bud flushing. *Quercus robur* showed the largest family variance components for bud flushing of all species in our Swedish study (estimates were comparable with those in the Lithuanian *Quercus robur* study at nursery stage), reaching on average 30%. But the magnitude of the family variance component for bud flushing varied between sites, being largest in southern trial.

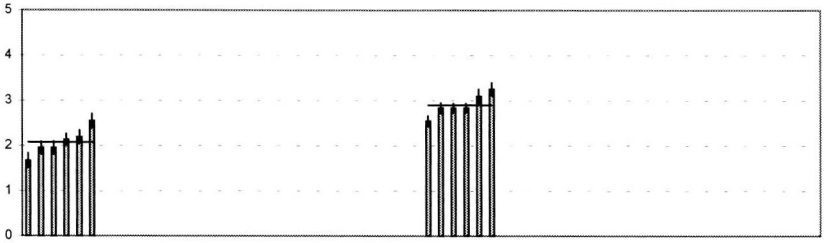
This was also the case for other traits in *Quercus robur* (*Fagus sylvatica* was studied only at one site). The largest values were obtained for northern populations at the southern site, while they were more or less equal at the northern site. The estimates for growth cessation and height traits were quite large, and stronger in *Quercus robur* than in *Fagus sylvatica*, but within each species they were of the same magnitude. Spring frost damage was considerable in southern populations of both species but was not observed at all in the northern trial.

The study of the Lithuanian *Quercus robur* populations (paper IV) revealed extremely high CV_As for bud flushing. The family variance components were also highest for bud flushing, although they decreased after replanting to field trials at age four. In contrast with the Swedish study, a much smaller family variance component was obtained for growth cessation with a magnitude of 6%, half as large as obtained for height. The CV_As for this trait did not differ much from those obtained in the Swedish experiment.

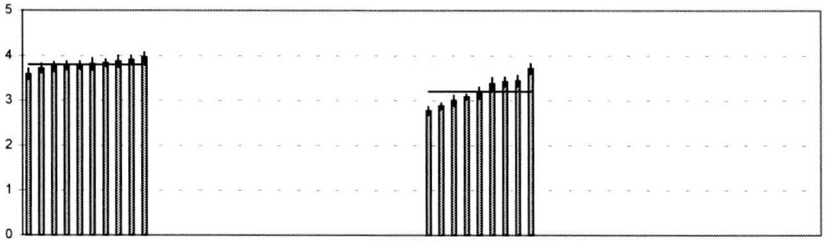
In the study of *Sorbus aucuparia* and *Prunus padus* (paper V) the largest family variance components were obtained for bud flushing, although in *Prunus padus* it was of the same magnitude as for growth cessation and height. The largest CV_As in both species were obtained for growth cessation. A tendency to some increase with age was seen both for bud flushing and growth cessation, while for height there was a remarkable decrease.



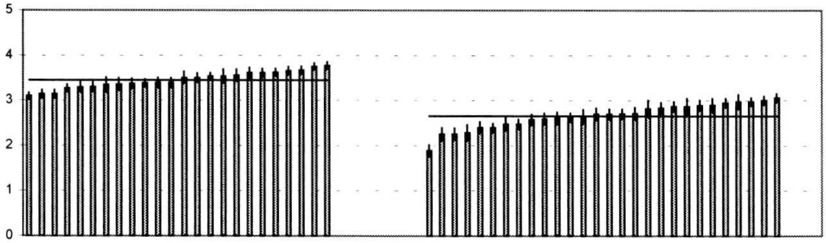
Alnus glutinosa



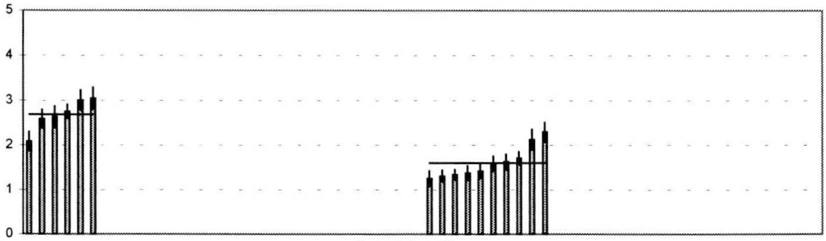
Sorbus aucuparia



Prunus padus

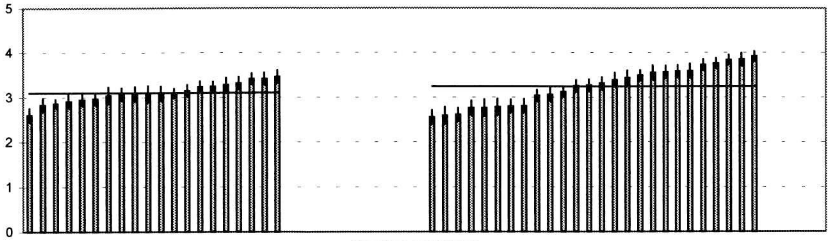


Prunus avium

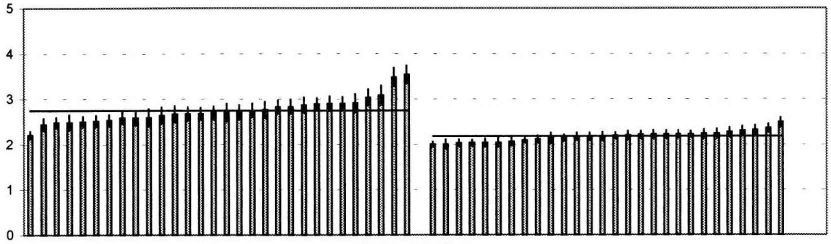


Acer platanoides

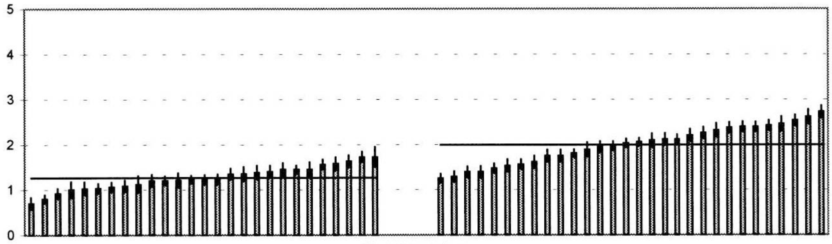
continued Fig. 2



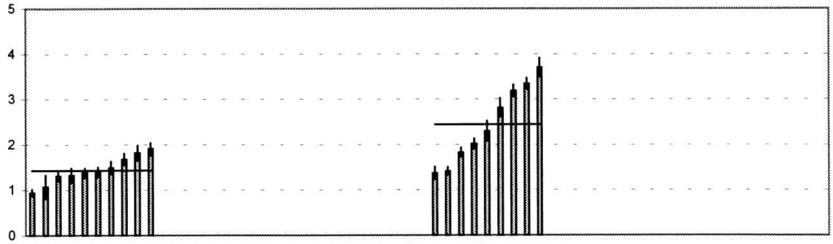
Fraxinus excelsior



Fagus sylvatica



Quercus robur

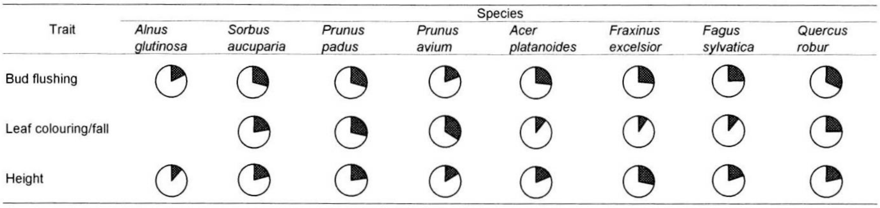


Lithuanian *Quercus robur*

Fig. 2. Mean values of open-pollinated families & populations in bud flushing at age 4 with the lowest and highest estimates of family variance components.

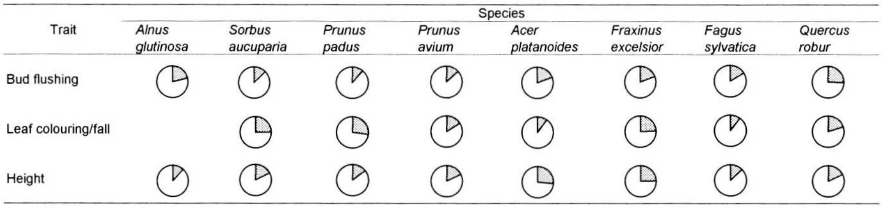
One way of synthesising the results from this study is shown in Tables 3 and 4, in which data from all recordings of the same types of traits were used to calculate the mean value for each species. The species were arranged according to the expected increase in within-population variation according to our hypothesis on the impact of life history traits on this variation. It should be noted that different numbers of recordings were taken in different species. The mean values of family variance components and CV_As for bud flushing agreed to some extent with the hypothesis while the results deviated to a certain degree for leaf colouring and height. The intermediate species, *Acer platanoides* and *Prunus avium*, showed larger family variance components than expected.

Table 3. The mean estimates of family variance components (derived from the estimates for separate populations) over all years in species from different experiments. Species are ordered from left to right according the expected estimates of family variance component



Trait	Species							
	Alnus glutinosa	*Sorbus aucuparia*	*Prunus padus*	*Prunus avium*	*Acer platanoides*	*Fraxinus excelsior*	*Fagus sylvatica*	*Quercus robur*
Bud flushing	◔	◔	◔	◔	◔	◔	◔	◔
Leaf colouring/fall		◔	◔	◔	◔	◔	◔	◔
Height	◔	◔	◔	◔	◔	◔	◔	◔

Table 4. The mean estimates of CV_A (derived from the estimates for separate populations) over all years in species from different experiments. Species are ordered from left to right according the expected estimates of family variance component



Trait	Species							
	Alnus glutinosa	*Sorbus aucuparia*	*Prunus padus*	*Prunus avium*	*Acer platanoides*	*Fraxinus excelsior*	*Fagus sylvatica*	*Quercus robur*
Bud flushing	◔	◔	◔	◔	◔	◔	◔	◔
Leaf colouring/fall		◔	◔	◔	◔	◔	◔	◔
Height	◔	◔	◔	◔	◔	◔	◔	◔

Thanks to the recording of bud flushing in the female trees in the Lithuanian *Quercus robur* study there was a unique opportunity to estimate the heritability of this trait via the parent-offspring relationship. As seen from Fig. 3 there was a strong relationship giving a heritability estimate of 0.88.

Correlations

Table 5 summarises the two types of estimates of genetic correlation within the trials: within the same trait in different years and between traits the same and different years. There were several trait combinations for which species performed almost the same, such as: bud flushing in different years, height at different ages and bud flushing with leaf fall. The first two of these combinations revealed strong relationship in juvenile trees and the last one, bud flushing with leaf fall, always showed weak correlations. Because of restrictions placed on the standard errors of family variance components in traits to be used for genetic correlation calculations, not all species were represented equally. Some species were not assessed for frost damage. It follows from the table 5 that the correlation of leaf fall in different years is strong for *Quercus robur* and *Prunus avium* at the juvenile age. *Prunus avium* showed a strong relationship between leaf fall or growth cessation and height. Bud flushing and spring frost were strongly correlated in *Quercus robur* and *Fraxinus excelsior*.

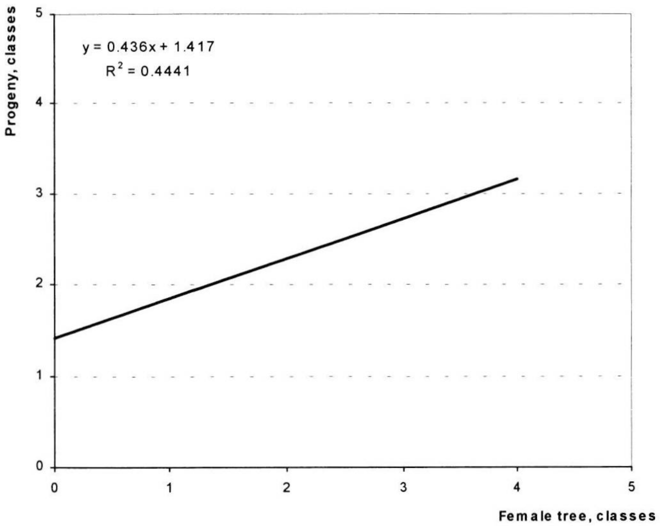


Fig. 3. Parent-offspring relationship in bud flushing of *Quercus robur*. Progenies are represented by open-pollinated family mean values. The acorns were harvested the same year.

Table 5. Summary of genetic correlation estimates for separate species, indicated by the first letters of their Latin name. Ag=Alnus glutinosa, Ap=Acer platanoides, Fe=Fraxinus excelsior, Fs=Fagus sylvatica, Pa=Prunus avium, Pp=Prunus padus, Qr=Quercus robur, Sa=Sorbus aucuparia

Trait relationship	Stregth of correlation		
	Strong	Moderate	Weak
Within type of trait:			
Bud flushing - bud flushing	*Pp, Sa, Fe, Pa, Qr, Fs, Ap, Ag*	-	-
Leaf fall - leaf fall	*Qr, Pa*	*Pp*	*Sa, Ap*
Height - height	*Pp, Sa, Fe, Pa, Qr, Ap, Ag*	-	-
Between type of trait:			
Bud flushing - leaf fall	-	-	*Pp, Sa, Fe, Pa, Qr, Fs, Ap*
Bud flushing - height	-	*Pp, Fe, Pa, Fs, Ap, Ag*	*Qr, Sa*
Leaf fall - height	*Pa*	*Pp, Fe, Qr, Ap*	*Sa*
Bud flushing - spring frost	*Qr, Fe**	*Pa*	*Fs**
Leaf fall - spring frost	-	*Pa*	Qr
Height - spring frost	-	*Qr, Fe**	*Fs**

* - the estimate derived from the family mean correlation.

Family mean correlations between and within traits of four broadleaves species (paper I) were strong and significant in bud flushing over years. There was a weak to moderate negative relationship of bud flushing with height in *Acer platanoides* and *Fraxinus excelsior*.

The only strong genetic correlation observed in *Quercus robur* in the Lithuanian study was the correlation between different trials of bud flushing at age 6; height was correlated moderately and leaf fall does not show any consistent correlation.

Only bud flushing in *Alnus glutinosa* showed significant correlation with geographic variables. Height was weakly correlated with geographic and meteorological variables in *Fagus sylvatica*, and weakly to moderately correlated with the variables in *Fraxinus excelsior*, although the strength of correlation in these two species was the opposite.

GxE interaction

The most extreme cases of site x family interaction for bud flushing and growth cessation are shown in Figure 4. The two populations deviating most in terms of interaction for growth cessation and two populations having less pronounced interaction for bud flushing are presented for both the Swedish and Lithuanian experiments. The figures are not very different for bud flushing in the different materials, but they are rather different for growth cessation. The difference between family variance components in two experiments is seen from the table 6. The figures for bud flushing and height are quite similar.

In the comparative study of *Fraxinus excelsior* and *Prunus avium* (paper II) the estimates of site x family interaction for bud flushing were large and significant only in the most southern populations of both species, but the interaction was large compared to the family component in *Prunus avium* populations. More family x site interaction was observed for leaf fall and growth cessation than for bud flushing in both species, and again the southern populations showed strongest interaction. The family interaction with site overtook family effect for height in *Prunus avium* and was quite large and mostly significant in *Fraxinus excelsior*.

In paper III we only had the possibility to calculate site x family interaction for *Quercus robur*. Only one population showed significant interaction in bud flushing. The estimates for growth cessation were large, especially for southern populations, but the largest estimates were obtained for height. Only the northern most population showed no significant interaction in any trait.

Some results for family plasticity of open pollinated progeny at the juvenile stage are presented in IV. The number of families contributing significantly to the ecovalences for bud flushing in the Lithuanian populations of *Quercus robur* was around 22% of total number, but only 13% of families in the case of growth cessation (paper IV). Around one third of families showed significant and high ecovalence in height, as was expected.

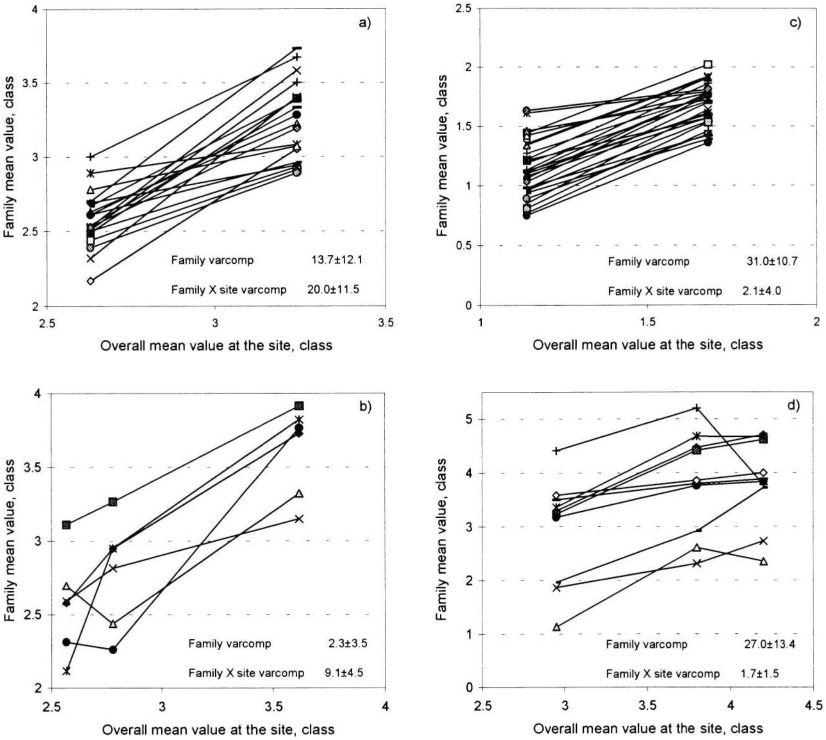


Fig. 4. The most extreme cases of site x family interaction for bud flushing, which show almost no effect (pictures c, d), and the largest estimates for growth cessation (pictures a, b) among the *Quercus robur* populations in the Swedish (pictures a, c) and Lithuanian studies (pictures b, d).

Table 6. Variance components of family and site x family interaction in Quercus robur studied in Sweden and Lithuania

Trait	Experiment series	Variance components of random effects, %	
		σ_f^2	σ_{sf}^2
Bud flushing	Lithuania	15.8±3.9***	1.1±0.8
	Sweden	13.5±2.5***	2.5±0.9**
Autumn leaf colouring	Lithuania	0.7±0.8	3.6±1.3**
	Sweden	7.5±1.6***	3.8±1.0***
Height	Lithuania	6.7±2.3**	6.0±1.5***
	Sweden	3.5±1.2**	4.8±1.2***

Among-population genetic variation

The population variance components increased with age and were highest for bud flushing in three of four broadleaves species, namely *Acer platanoides*, *Alnus glutinosa* and *Fraxinus excelsior* (paper I). They also increased in population effect proportion to family one. *Fagus sylvatica* did not show any population effect in bud flushing. The population variance components for growth cessation were much smaller than for bud flushing and generally larger than family estimates. A slight decrease in population variance components was observed for height, though it was always significant. The only exception was *Fraxinus excelsior*, in which population effect almost doubled.

In the Lithuanian study of *Quercus robur*, the population variance component estimated for bud flushing was extremely high (paper IV). For growth cessation it was small compared to the family variance component. Height did not show any population effect. From figure 5 it can be seen that large differences in population means for bud flushing exist in Lithuanian *Quercus robur*, while the differences in height are small and not significant. The evidence is that Swedish populations differ much more in mean values for growth cessation than do Lithuanian populations.

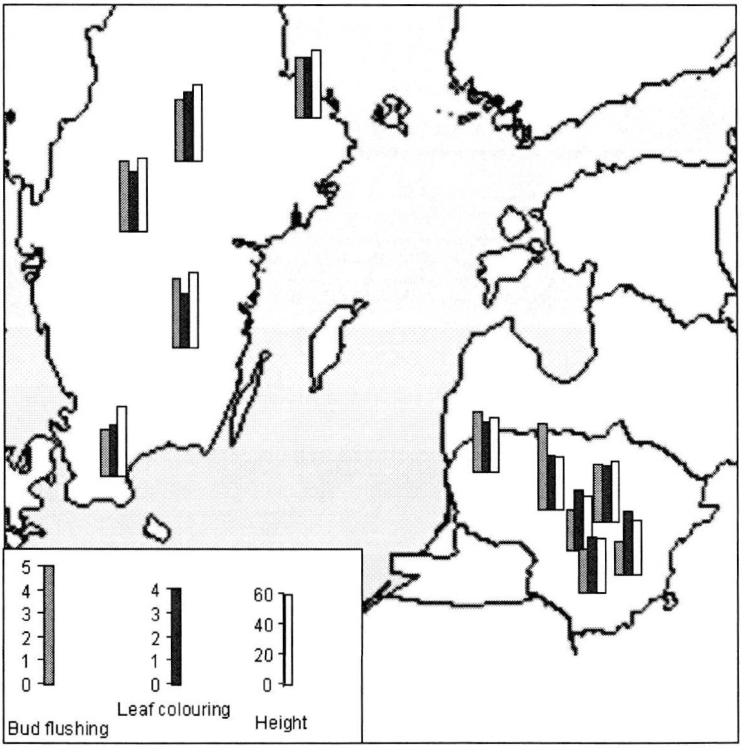


Fig. 5. Swedish and Lithuanian *Quercus robur* population means for bud flushing, leaf colouring and height at ages 3 and 4 (height of the Lithuanian populations at age 3).

DISCUSSION

Limitations of the study

The number of populations and families in different species included in this study varied from species to species. The main reason for this was insufficient seed production in stands in some regions. The years in which cropping occurs and intervals between the crops, and the longevity of viable seed storage are different in each species, and so it was complicated to get samples from some species simultaneously. The varying number of families in the populations of different species also reflected the present situation in Swedish natural stands, suggesting that not enough seed-bearing trees were available for each species in some stands. The requirement of a minimum distance of 40-50 meters between the trees made sampling sometimes still more complicated, but at the same time it decreased the probability of genetic identity and let us approach the structure of the population with a limited number of representatives. That was analysed for phenotypic structure of bud flushing and was confirmed in the Lithuanian *Quercus robur* study (Baliuckas & Pliura 2000). The study of genetic structure in *Quercus robur* and *Quercus petraea* stands revealed a significant decrease in genetic distance between the trees at a distance of 30-50 meters (Cottrell et al. in press). Since this study, especially in Sweden, was more basic than applied gene conservation, the size of the material analysed was satisfactorily large (papers II and III). Two species, *Fagus sylvatica* and *Fraxinus excelsior*, were represented by only three populations per experiment, and participated in two experiments with different populations included.

To illustrate the scale of the work performed at the time of assessments, we remark that, for example, in the assessment of four species (analysed in the papers II and III) in the largest experiment there was a need to make recordings of over 15000 seedlings at one site (Öland) at each assessment. In order to get better precision in assessments of the progenies for growth rhythm traits, two or even three recordings per trait/season were performed. Only one person carried out all work in the Swedish experiments, so the precision of assessments was free from any bias introduced by recordings carried out by different persons. We aimed for a linear scale but it is always a problem to obtain full linearity for traits which are dependent on the ambient weather conditions.

There were several reasons for making fewer assessments at the northern site in the experiments with *Quercus robur*, *Fagus sylvatica*, *Fraxinus excelsior* and *Prunus avium*. The severe damage by voles, spring frost and summer drought were among the major limiting non-genetic factors, although those factors did not all equally affect all species. This resulted in a lower number of G x E estimations than planned.

The site conditions in the Öland trial (paper II and III) were very uniform at this site. The competition of seedlings with weeds in the very early stages of experiment establishment was the only negative factor. The location of the site in the first experiment (described in paper I) could be questionable in the light of the aim of the study as only one of four species analysed there had more northern population origins than the site location.

Populations were separated by sub-blocking in the experimental design of three out of four Swedish studies (II, III, and V). The reason for this was that the funding agency required that the trials should be converted to seedling seed orchards once they reach appropriate age. The statistical model used in paper V allowed an analysis of the population effect thanks to the common location of all populations of one species. This option could not be used in papers II and III since populations of each species were separated from one another.

The calculation of CV_As was recommended by Houle (1992) to provide information on the long-term potential for adaptation. However, there is a problem with CV_As for non-continuous traits since the estimates are dependent on the mean value (the numerator in the calculation of CV_A) of the trait. Linearity of the scale used is also required. These limitations make it hard to compare CV_As between traits.

Agreement with the hypothesis

Table 3 was constructed in order to examine whether the results were influenced by the life history traits of the species studied. It should be noted that Lithuanian data on *Quercus robur* are not included in Table 3. The within-population variation in bud flushing increases slightly from pioneer to intermediate species. There is no such trend for growth cessation and the varying magnitude of estimates will also be discussed for separate species. The mean estimates of family variance components for height were fairly similar in all species, though some increase is seen in values in the right-hand part of Table 3. One possible reason for the absence of any clear trend from pioneer to climax species may be that gene flow among populations is much larger than expected even in species which are neither wind-pollinated nor have a wide and continuous distribution. Thus recent data from studies of the two insect pollinated species, Sorbus torminalis (Demesure et al. 2001) and *Acer platanoides* (Mari Rusanen pers. Comm.) indicate that gene flow in both cases is substantial. If this is the case, the within-population variation will also be greater than expected. Another possibility is that there is preferential mating within small cohorts within a population. If this occurs over several generations, trees within a population will be related and the assumed half-sib relationship of the material studied will not be totally valid. The presence of a higher degree of relatedness than half-sibs will lead to exaggeration of the heritability. Because of this, Sæbø and Johnsen (2000), in their study of *Prunus padus* and *Sorbus aucuparia*, assumed that the relatedness of their open-pollinated families was closer than true half-sibs. Such a mating pattern would be less frequent in a continuously distributed and wind-pollinated species. Both explanations would reduce the difference between species with contrasting life history traits.

Almost no trends could be identified for CV_A for any of the traits, but some uniformity could be detected in the estimates of all traits within individual species. As CV_A is a property of a population, it is also useful to examine the population estimates and not only mean values for species. In general, it could be concluded that the largest within-population variation, regardless of species, occurred for bud flushing, the next position being shared by growth cessation and height.

The more detailed study of population differentiation within the species showed that northern populations of *Quercus robur*, *Fraxinus excelsior* and *Acer platanoides* had larger within population variation in growth rhythm and height traits than southern ones, independent of the trial. The estimated within population genetic variation in *Fraxinus excelsior* at the northern site for a given trait at similar age was more pronounced than at the southern. The opposite was observed in *Quercus robur*. None of these species can be regarded as pioneers, so cultivation in open area can lead to misleading conclusions about adaptation. It seems that habitat conditions are of great importance for *Fraxinus excelsior* at northern latitudes, causing maladaptation of local populations if grown at improper site. The small variance components for growth cessation in *Fraxinus excelsior* and *Acer platanoides* to some extent reflect the adaptation of species to a balance between photoperiod and temperature in the induction of the process that triggers growth cessation. The insufficient number of populations studied in these species reduce our ability to make any inferences on clinal variation for this trait, but in *Fraxinus excelsior* in particular there was a large difference in population mean values. It could be expected that 'southern' species would react more to temperature regime than photoperiod, though the importance of photoperiod/temperature ratio for growth cessation may change exponentially character from south-north, the first having increased importance at northern latitudes (Clapham et al. 2001). A small proportion of all QTLs detected for bud flushing in Pseudotsuga menziesii were detected at different sites, indicating that geographic location plays an important role in the start time of spring growth (Jermstad et al. 2001).

Parent-offspring relationship

To our knowledge there are few studies of this kind for forest trees. A strong parent-offspring relationship in bud flushing indicates that assortative mating prevails in *Quercus robur* stands. The high regression coefficients obtained were a result of the diversity of phenological forms for bud flushing in the separate stands, becoming extremely high when a broad span of forms was present (as is evident from the Figure 2). The study of genetic differentiation between mature *Quercus robur* stands and their progeny, based on isozymes, revealed higher genetic differentiation between the seedling samples than between mature stands (Gehle 1999). We do not exclude the possibility that progeny raised from crops harvested in different years would give quite different results. An isozyme study performed on *Fagus sylvatica* seed crops from the same stand harvested in two different years revealed significant differences between the seed lots (Ziehe et al. 1998). As a corollary of this, the isozyme pattern of one seed crop only agreed with the genetic structure of the adult stand.

GxE interaction

The estimates obtained for site x family interaction in three species, *Quercus robur*, *Fraxinus excelsior* and *Prunus avium*, showed that southern populations interacted to a larger extent than northern. The largest ratio of estimated variance for site x family interaction to total variance was obtained in *Prunus avium*. The extremely large site x family variance component for growth rhythm and height traits in the southernmost *Prunus avium* population suggest the presence of some specific adaptation, or lack of adaptation, to comparatively harsh site conditions in this species. There was no indication that population origin could have influenced the block x family effect in any trait. The largest mean estimates, regardless of species, were obtained for height, but varied from population to population. The proportion of site x family variance to family variance was small for bud flushing in *Quercus robur* studies (Table 6). Large latitudinal range possibly influenced the differences in the family component for growth cessation in the two countries.

The highest estimates for block x family interaction for growth rhythm traits in the Lithuanian study of *Quercus robur* (paper IV) were obtained at the 'continental' sites, indicating that climatic conditions impact on within site variation. As was noted above for the three species in the Swedish study (II and III), the results from the Lithuanian *Quercus robur* study agreed, in that the largest site x family interaction was obtained for height. Despite the minor effect of site x family interaction for bud flushing, the proportion of families significantly contributing to the ecovalences was higher for this trait than for growth cessation. The reason could be the large variation in growth cessation at family level for height while the variation was limited for bud flushing.

Genetic correlations

Except for growth cessation in some species, the within trait genetic correlations for growth rhythm and height were strong and quite stable over years (see Table 5) indicating that one year assessments are fairly reliable. Moreover, given the strong parent-offspring relationship for bud flushing in the Lithuanian *Quercus robur* study, it could be suggested that juvenile-mature correlation can also be expected to be high. It is noteworthy that height ranks in female trees within populations and between progeny (as family mean) within populations at age 6 resulted in the parent-offspring correlation estimated at 0.38 with a 1% significance level (paper IV).

Correlations between bud flushing and leaf fall were almost always weak in all species. The polycyclic growth at juvenile trees, especially typical for *Quercus robur*, could make a large impact on this relationship. The estimation of variance components or analysis of variance for growth cessation usually reveals pronounced block effects within a site. Thus, there are several non-genetic factors that influence the possibility of tracing any significant relationships. The duration of the growing season is largely responsible for height growth. As growth cessation usually takes a longer time span and so has more influences on the duration of growing season than bud flushing, it seems natural that we mainly observed moderate association between height and growth cessation. Spring frost usually has a large effect when associated with bud flushing. The stage of bud flushing at time of frost occurrence has a crucial effect, but the plants which flush latest do not always have the advantage as regards spring frost damage due to fluctuation in time of frost occurrence.

Population differentiation

The unexpectedly small family variance components for bud flushing and height in some *Fagus sylvatica* populations and the absence of population effect could be attributed to several causes: 1) among-population variation is almost absent due to the limited range of populations origins; 2) a possible bottleneck effect at the northern limit of natural distribution (see Demesure et al. 1996) and 3) low differentiation due to relatively recent in evolutionary terms, establishment of those populations from limited founder populations. To verify this, populations from a wider range outside Sweden should be investigated.

The differences in mean of population variance components for bud flushing in the two countries (Fig. 5), suggest that there are probably some biotic factors causing large among-population variation in Lithuania. From the study of haplotypes in *Quercus* spp. (Jensen et al. 2002, Csaikl et al. 2002) it is evident that during postglacial migration, populations of *Quercus* species migrated to Sweden and Lithuania from different refugia. The study of the influence of lineages on phenotypic performance in a series of provenance experiments revealed a significant effect of cpDNA lineage on only 7 out of the 62 phenotypic traits studied, 5 of which were related to height, and also survival and leaf retention (Kremer et al. 2002). The general conclusion was made that differences in height growth of provenances from different lineages are stable. There were no species specific haplotypes found in the study of cpDNA in Europe, but the genetic distances presented were among the largest between the haplotypes found in Lithuania and Sweden. Five populations from the Lithuanian study were identified for cpDNA haplotypes. Interestingly, the population in which bud flushing was most variable (shown in Fig. 4) had a haplotype rare in Europe and the latest flushing population detected in the Lithuanian study had a haplotype originating from an Italian refugium. There were almost no differences in height of populations in relation to the difference in haplotypes.

The variation among populations for growth cessation in the Swedish study was so large that it probably represents real differences between populations, although the experimental design did not allow testing of population differences (cf. Table 2 in paper III). Explanations for the differences between the Swedish and the Lithuanian *Quercus robur* studies could either be that the latitudinal range of population origins were much larger in the Swedish study than in the Lithuanian or that species hybrids (*Q. robur* x Q petraea) were present in the southern Swedish populations.

Implications for gene conservation

The mean CV_As of the various species indicate the possibility for species in Sweden to respond to environmental changes in the long-term. The inclusion of populations with small CV_As for adaptive traits in gene conservation programmes will need more careful selection than for those with high CV_As, for example, in *Prunus avium* compared to *Quercus robur* (Table 4). The low number of populations means that the possibility to disclose population effects is limited. The estimates of the population variance component in growth rhythm traits could be used for decisions concerning the number of populations that ought to be included in the gene conservation of species. The larger the estimate, the more arguments can be found for inclusion of a larger number of populations for the species. In our case, the large population effects in *Acer platanoides* or *Fraxinus excelsior* indicate that larger number of populations need to be selected for gene conservation than in species such as *Fagus sylvatica* or *Prunus avium*. The clinal variation in adaptive traits in some of the species, such as *Alnus glutinosa*, means that populations for gene conservation have to be selected along the gradient detected, and the selection depends on the steepness of the gradient. The high CV_As for bud flushing in northern as well a sin southern populations of *Alnus glutinosa*, *Acer platanoides*, *Fraxinus excelsior*, *Quercus robur*, *Sorbus aucuparia* indicate that populations of both origin are equally useful for gene conservation. The level of naturally occurring introgression between related taxa, such as *Quercus robur* and *Quercus petraea* in southern Sweden need to be taken into account before making a final decision. The opinion that populations with a certain degree of introgression could be advantageous in case of climatic change was supported by various EUFORGEN networks.

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