Variation in Adaptive Traits in Broadleaved Species – with Special Emphasis on Climatic Adaptation

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Several forces are involved in determining the variation in adaptive traits of forest trees. Climate is assumed to be very influential, and as a consequence clinal variation patterns in frost hardiness, and onset and cessation of growth over climatic gradients have been frequently reported. The variation in adaptive traits between adjacent populations, however, is less than within populations in species studied, but the ratio might depend on the species position in the ecosystem. Thus, life history traits such as distribution, pollination vector and seed dispersal ability is thought to be important, and composition of these traits may partly predict the distribution of genetic variation within and among populations. It is likely that the broadleaves have a diverse genetic architecture because of the unique composition of life history traits of the individual species. Most native broadleaves in the Baltic and Nordic countries reach their absolute northern distribution limit in this area. With conifers there is little empirical support for the hypothesis of less variation in adaptive traits in marginal than in central populations, which possibly also applies for broadleaves. This could be due to variable selection, and for some species, perhaps asymmetric gene flow. A global increase in temperature is predicted to increase the distribution of broadleaves in Europe, at the expense of conifers. Though several life history traits are positively influenced by increasing summer temperatures, the rate of temperature change may be too rapid for adequate adaptation and dispersal of some broadleaved species.

Key words: adaptation, clinal varation, growth rhythm.

Introduction

In northern areas the overall variation in adaptive traits in native tree species is assumed to be strongly influenced by climatic constraints. Onset of the growth in spring, cessation of the growth in late summer and development of frost hardiness are under strong genetic control, and the timing of these phenological events is very critical for reproduction and survival.

Most of our tree species are broadleaves, but with few exceptions broadleaved species are poorly characterised with respect to variation in adaptive traits. Main emphasis in genetic research in northern Europe has been devoted to conifers because of their dominating role in the commercial forestry. However, over the last decades the awareness of and interest for minor species has increased owing to decline problems such as the Dutch elm disease and other threats to genetic resources. In addition, the broadleaves have unique aesthetic and recreational values. We have some information about commercial important broadleaves such as *Quercus* (Liepe, 1993, Ducousso et al., 1996), *Fagus* (Muhs, 1985, von Wuehlish et al., 1995) and *Betula* (Håbjørg, 1972, 1978, Myking, 1999) concerning variation in adaptive traits over geographic clines, and variation between and within populations. This kind of information is important both for conservation activities, utilisation and breeding and can not be deduced from variation patterns described for conifers. On the other hand, the knowledge about *Tilia, Alnus, Sorbus, Ulmus, Corylus* and *Fraxinus* is limited or totally absent.

This paper aims to give an outline of the current knowledge of distribution of genetic variance among and within populations in broadleaves species, particularly at the northern distribution edge. Variation in adaptive traits is also discussed in relation to global warming.

Distribution of genetic variance
Clinal variations

In many broadleaved species from the temperate and boreal region daylength is the cue for cessation of apical growth in late summer (Warcing 1956). Sylvén (1940), studying *Pinus sylvestris* and *Populus tremula*, was the first to demonstrate that the critical daylenght for growth cessation is longer in northern than in southern provenances of the species. Whereas the critical daylength in a northern provenance of *Betula pendula* from Finnmark in Norway (69°30'N) is between 22 and 24 h, a southern provenance from Denmark (56°20'N)

ceases growing at about 16 h photoperiod (Håbjørg 1978). However, because daylength is a function of latitude, cessation of growth takes place at about the same time in different provenances in their native environments. After Sylvéns remarkable discovery (1940), difference in critical daylength for growth cessation over latitudinal clines has been demonstrated in numerous species, including many broadleaved species (Table 1). According to Håbjørg (1978) growth cessation is fairly synchronous in different species at a given latitude, but as will be discussed later, there is a pronounced variability within populations for this trait.

Clinal variations have also been demonstrated in the timing of growth resumption in spring (Table 1). Budburst occurs generally later in provenances native to mild winters than in provenances from areas with cold and stable winters (Myking, 1999). In Scandinavian *Betula* species this corresponds to clines from south to north and from coast to inland (Myking and Heide, 1995, Myking, 1997), and in central Europe *Fagus sylvatica* and *Quercus* spp. similarly display a cline from the interior of the range to the coast in north-west (Liepe, 1993, von Wuelish et al., 1995). The importance of such variation patterns has clearly been shown in *Quercus petrea* where continental provenances from Hungary and Austria suffered severely from spring frost damages when planted closer to the northern range near the coast, such as in Denmark and Britain (Liepe, 1993). It is remarkable, however, that the latitudinal trend in timing of budburst in *Quercus petrea* and *Fagus sylvatica* is opposite to that shown in conifers and other broadleaves where late flushing is most typical in the south (Liepe, 1993, von Wuelish et al., 1995, Kremer et al., 1998). Such differences may depend on the specific latitudinal trends in the climatic factors to which the various species have been adapted.

The above results show that timing of onset and cessation of the growth conform to overall clines in photoperiod and temperature. Such clinal trends have been demonstrated in species with very different life history traits, including insect- and wind pollinated species, widespread and scattered occurring species, and species with effective and less effective seed distribution (Table 1 *vs* Table 2). Apparently, there is sufficient genetic variation even in small populations to develop adequate timing of the growth rhythm. Alternatively, the clinal trends were developed during the post-glacial warming when the populations were larger and it was more variation available for adaptive processes to occur.

Table 1. Examples of clinal variations in two adaptive traits. Critical photoperiod refers to variation along latitudinal clines only, whereas timing of growth resumption refers to variation both along latitudinal (N-S), coastal - inland (C-I), and altitudinal gradients (Alt).

Critical photoperiod for growth cessation		Timing of growth resumption	
Populus tremula	(Sylvén 1940)	*Betula* ssp.	N-S, C-I, Alt (Myking and Heide 1995, Leinonen 1996, Myking 1997)
Alnus incana	(Vaartaja 1954, Håbjørg 1978)		
Betula	(Håbjørg 1972, 1978, Myking and Heide 1995)	*Fagus sylvatica*	N-S, C-I, Alt (Muhs 1985, Madsen 1995, von Wuehlich et al. 1995)
Acer platanoides	(Westergaard 1997a)	*Acer platanoides*	N-S (Westergaard 1997a)
Salix caprea	(Håbjørg 1978)	*Quercus robur*	N-S (Jensen 1993)
Corylus avellana	(Håbjørg 1978)		
Ulmus glabra	(Håbjørg 1978)	*Quercus petrea*	N-S, C-I, Alt (Liepe 1993, Deans and Harvey 1996, Ducousso et al. 1996, Stephan et al. 1996, Kremer et al. 1998)
*Sorbus aucuparia**	(Håbjørg 1978)		
		Fraxinus excelsior	N-S Kleinschmit et al. 1996
		Sorbus aucuparia	C-I (Erstad 1999)

* The presence of clinal variation patterns in critical photoperiod for growth cessation in *Sorbus aucuparia* is questionable (cf. Håbjørg 1978).

Table 2. Life history traits assumed to influence the genetic structure of tree species (Eriksson 1992). Increasing genetic variability within populations with increasing number of characteristics to the right hand side in the table.

Trait	Characteristic
Distribution	scattered – continuous
Population size	small - large
Pollination vector	insect – wind
Seed dispersal	limited – effective
Reproduction	vegetative – sexual
Habitat specificity	specialised – broad
Position in the ecosystem	climax - pioneer

Within/ between population variation

When considering the issue of distribution of genetic variability, the geographic span always has to be taken into consideration. The above studies show that the difference in timing of resumption and cessation of the growth in distant populations may be pronounced. This is usually the case even though such clinal trends usually refer to population means which mask the variability within populations. Between adjacent populations, however, the within-population is usually greater than the between population variation. This appears

to be a general feature of both broadleaved species and conifers (Skrøppa and Johnsen 2000, Sæbø and Johnsen 2000). There is evidence, however, that the ratio of within to between population variation varies between species (Baliuckas et al., 1999).

It is generally assumed that composition of life history traits affects the distribution of genetic variance between and within populations (Table 2). Broadleaved species are much more diverse in terms of life history traits than our native conifers and are thus expected to be more variable with respect to genetic structure. The highest genetic variability within populations would be expected in species with wide and continuous distributions, wind dispersal of pollen and seeds such as *Betula* and *Alnus*. This is comparable to the pattern described in conifers (Eriksson, 1992). *Alnus glutinosa* is a wind-pollinated rather widespread species with effective seed dispersal, whereas *Acer platanoides* has a more narrow and scattered distribution, is pollinated by insects and has comparably heavy seeds. At the age of three there was a consistent tendency for greater differentiation of populations and families in *Acer platanoides* than *Alnus glutinosa* for bud flushing, growth cessation and plant height (Table 3). This might be associated with non-random mating and limited gene flow between populations and families of *Acer platanoides*. *Fraxinus excelsior*, which is comparable to *Acer platanoides* with respect to life history traits, displayed about the same variation pattern as *Acer platanoides* (Baliuckas et al., 1999). Species with extensive exchange of pollen and seeds over large distances maintain more variation within population than species with limited

Table 3. Percentage variance components for different traits at the age of three for *Acer platanoides* and *Alnus glutinosa* (Baliuckas et al., 1999). Both at the population and family level *Alnus platanoides* is more differentiated than *Alnus glutinosa*.

	Bud flushing		Growth cessation		Plant height	
	Population	Family	Population	Family	Population	Family
Acer platanoides	14.4	12.8	5.0	6.3	9.2	5.4
Alnus glutinosa	11.4	8.2	3.4	2.7	3.6	3.0

gene flow. *Picea abies* is a good example of a conifer of the first category (Skrøppa and Kohmann, 1997), and *Betula pendula* behaves like spruce in this respect (Skrøppa pers. com). Accordingly, variation patterns in adaptive traits appear to be partly predictable with basis in composition of life history traits.

Genetic variation at the distribution edge

This is a pertinent issue since most of our native tree species reach their northern distribution limit in the Nordic and Baltic countries. Most broadleaved species have scattered occurrences, even in central parts of the distribution. Stochastic forces associated with small population sizes near the distribution edge such as inbreeding and genetic drift may thus be even greater than for conifers and could lead to non-adaptive differentiation. On the other hand, strong directional selection pressure due to climatic constrains could increase the adaptive differentiation in marginal populations, with the cost of decreased genetic variation. However, there is limited empirical support for the hypothesis of lower variation in marginal than in central populations (Tiegerstedt, 1994, Savolainen, 1997, Eriksson, 1999).

Tiegerstedt (1994) argues that high genetic variation in marginal populations could be maintained by variable selection. Asymmetric gene flow would also contribute to the high genetic variability in marginal areas. In *Pinus contorta*, a net flow of less hardy genotypes from the centre to the periphery is suggested to be the reason why marginal populations are skewed toward greater growth at the distribution edge than what is expected to be optimal (Rehfeldt et al., 1999, Rehfeldt, 2000). There is evidence for the same phenomenon in *Pinus sylvestris* in Sweden associated with the substantial pollen flow from the south in spring (Lindgren et al., 1995). If present in hardwoods, the effect is likely most pronounced in wind-pollinated, dense populations of species with wide occurrences such as *Betula* species which have very light pollen, and perhaps *Alnus*. Asymmytric gene flow is not likely to occur in insect pollinated species in *Sorbus*, *Acer*, *Prunus* and *Tilia*.

Possibly there is no such thing as adaptive perfection. The environment of forest trees is variable in time and space, and a substantial gene flow which maintains high within-population variation antagonises adaptation by natural selection (Eriksson 1999). Thus, different evolutionary forces have opposing effects on the genetic variation patterns of forest trees, and the strength of the individual evolutionary forces depends on the life history traits of a species. In the context of adaptive perfection phenotypic plasticity operates as a stabilising force which reduces negative effects associated with small effective population sizes and limited and asymmetric gene flow. On the other hand, phenotypic plasticity reduces the efficiency of natural selection (Eriksson, 1999). We have very little information

about phenotypic plasticity in broadleaves, but it is generally expected to be large in long-lived species such as forest trees (Eriksson, 1999).

Global warming

Climate exerts a major control over the distribution of forest trees. The most dramatic evidence for this view comes from pollen-based reconstruction of changes in tree species distributions during the post-glacial period. Analyses of historical records suggest that periods of several hundred to several thousand years are required for significant change in vegetation. However, changes in frequency, severity, or magnitude of disturbances may well occur (Loehle and LeBlanc, 1996). Following a doubling of the CO_2 concentration the global mean temperature may increase 1.5 to 4.5°C. The greatest warming is expected during winter, and once initiated the warming is expected to be completed within a century (Loehle and LeBlanc et al., 1996). It is likely that budburst and flowering may take place earlier after a global warming than at present, with an increased risk of frost damage in spring (Myking and Heide, 1995, Eriksson, 1999).

Speed of evolution has a prime importance for species survival under a global warming (Eriksson, 1999). The evolutionary process depends on the additive variance within populations which in turn is affected by dispersal of pollen and seeds, mating pattern and mutation rate. Fertile age and seed yield also affect the speed of evolution (Table 4). Beside its direct effect on the speed of evolution, dispersal ability is important for changing the distribution range in response to climatic changes. This ability is probably lowest in species with heavy propagules (Eriksson, 1999). Thus, it appears that *Tilia cordata,* which has almost complete sterility of seeds in northern Europe (cf. Pigott and Huntley, 1981), has the lowest adaptability to future changes in climate, but also species of *Acer, Fagus* and *Quercus* could be exposed (Table 4). *Betula, Alnus* and *Salix* species, on the other hand, are assumed to have the best adaptive potential owing to wide distributions, effective dispersal of pollen and seeds, frequent and large seed yield and low fertile age.

In *Picea abies* and some other conifers it has been shown that high temperatures during the reproductive process produce offspring with longer growing season and later bud set than progeny produced after at low temperatures (Skrøppa and Johnsen, 2000). Following global warming pollination will take place at higher spring temperatures, and bud set would probably be

Table 4. The speed of evolution depends on the additive variance (Eriksson, 1999) which in turn is hampered by the traits below. The overall gene flow depends primarily on the distribution, the effective populations size, vector for pollination and seed dispersal, and mating pattern. This approach leaves *Tilia* as an exposed species, whereas *Acer, Quercus* and *Fagus* take an intermediate position. Genera such as *Betula, Alnus, Salix* and *Corylus* are assumed to have the best capability for evolutionary change following a global warming.

	Speed of evolution			
	limited gene flow	high fertile age	limited seed set	limited seed yield
Fraxinus		x		x
Acer	x	x		x
Ulmus		x		
Quercus	(x)	x		x
Sorbus	x			x
Tilia	x	x	x	x
Fagus	(x)	x		(x)

delayed accordingly. If such after-effects of temperature operate in broadleaved species as well, it could in the short term perspective create a new and inappropriate balance between photoperiod and temperature leading to increased risk of frost damages in autumn. Investigations are planned with *Betula pendula* to see whether different temperatures during seed production have similar effects as in *Picea abies*. A next step would be to study more boadleaved species for this phenomenon (Johnsen pers. com.).

Some compensating mechanisms to negative effects of global warming need to be outlined. The first is phenotypic plasticity. If global warming takes place within a century, most boadleaved species will not be able to respond by shifting gene frequencies because of long generation turnover. Modulation of the phenotype may thus have a pronounced adaptive significance in the short-term perspective. A second mechanism is the effect of autumn temperature on the timing of dormancy release that is found in *Picea abies* and *Acer platanoides* (Heide, 1974, Westergaard, 1997b). In these species high temperatures following dormancy induction in late summer delayed dormancy release and budburst the subsequent spring. If this is a general feature of forest trees it can have importance for avoidance of frost damages in spring following global warming. In addition to these compensating mechanisms, it must be emphasised that

the present summer temperatures are a main constraint to distribution of forest trees, in particular noble hardwood species. Accordingly, global warming would be highly positive for a number of life history traits which affect the speed of evolution, such as the generation turnover, seed crop, seed set and gene flow. Many broadleaved species are thus expected to increase the distributions in northern Europe following global warming (Sykes and Prentice, 1996).

Conclusions

Climate is a dominating force in determining the genetic variation of broadleaved species and other forest trees, and for traits related to growth rhythm clinal variation patterns have been frequently reported, irrespective of the species ecological status. The broadleaves is a very diverse group of species that differ in many life history traits, and there is support for the view that wind pollination in combination with effective seed dispersal maintains larger within population variation than insect pollination and less effective seed dispersal. Climatic adaptation in some broadleaves might be hampered by asymmetric gene flow, and adaptability to global warming might be least in species with fragmented populations of species with low dispersal ability and limited additive variance such as some noble hardwoods.

Acknowledgement

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