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Gene Flow and Local Adaptation in Trees

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Key Words

cline, natural selection, provenance trial, polygenic variation,
migration

Abstract

Populations are locally adapted when populations have the highest relative fitness at their home sites, and lower fitness in other parts of the range. Results from the extensive experimental plantations of populations of forest trees from different parts of the range show that populations can survive and grow in broad areas outside the home site. However, intra- and interspecific competition limit the distribution of genotypes. For populations from large parts of the range, relative fitness, compared with the local population, is often highest at the home site. At the edges of the range, this local adaptation may break down. The extent of local adaptation is determined by the balance between gene flow and selection. Genetic differentiation and strong natural selection occur over a range of tens or hundreds of kilometers, but reliable measurements of gene flow are available only for much shorter distances. Current models of spatially varying selection could be made more realistic by the incorporation of strong selection and isolation-by-distance characteristic of tree populations. Many studies suggest that most variation in adaptive traits is based on loci with small effects. Association genetics methods and improved genomic resources are useful for the identification of the loci responsible for this variation. The potential for adaptation to current climate change depends on genetic variation and dispersal and establishment rates.

INTRODUCTION

The evolution of adaptation has received increasing attention in recent years. Theoretical work has generated new predictions on the genetic dynamics and architecture of adaptation (Orr 1998). Specifically, local adaptation (Kawecki & Ebert 2004) and adaptation to clinally varying environments have been addressed (Barton 1999). Genetic tools, such as quantitative trait locus (QTL) mapping (Tanksley 1993) and association studies, are now available for the study of the genetic basis of adaptation. The study of sequence variation also provides means to detect loci responsible for local adaptation (Wright & Gaut 2005). Ongoing climate change has increased interest in the ability of species and populations to adapt to new environmental conditions (Houghton et al. 2001). These developments led to new approaches in the study of adaptation of trees.

Tree species occupy shifting geographic ranges, as documented in pollen and other fossil records (Huntley & Birks 1983, Willis & van Andel 2004). Range expansions and contractions have left their marks both in the plastid DNA and the nuclear genes of current populations (Heuertz et al. 2006, Petit et al. 2003). Comparisons of molecular and quantitative data suggest that recent selection, which occurred after postglacial colonization, is the predominant factor that shapes present quantitative trait variation (Collignon et al. 2002, Kremer et al. 2002).

Local adaptation can occur with respect to many selective factors, such as climate, edaphic factors, and parasites (Hedrick 2006, Kawecki & Ebert 2004, Linhart & Grant 1996), and different traits can respond to selection. Endler (1977) provides examples of small scale clinal variation in trees.

Foresters study adaptation with the establishment of common garden experiments at multiple sites; each contains many provenances (populations from well defined geographic areas) of the species. The goal of these studies is to find the most suitable provenances for planting in different environments. These studies provide extensive information on the effects of provenance transfers and genetic differentiation of tree populations (Langlet 1971, Morgenstern 1996).

In this review, we combine results from these classical studies on trees with evolutionary theory, new findings on migration, and recent extensive genetic work. Specifically, we ask the following questions: First, which genetic models of spatially varying selection are most relevant for forest tree populations? Second, how much gene flow can be detected with recently developed molecular tools? Third, do old provenance trials provide evidence of local adaptation? Fourth, what is the evidence for local adaptation from genetic differentiation studies in common garden experiments? Fifth, what is the genetic architecture of adaptive traits: many loci with small effects or fewer loci with larger effects? Last, is local adaptation possible at range margins, and can trees respond genetically to climate change caused by humans?

BACKGROUND FOR LOCAL ADAPTATION

Spatial variation in the pattern of natural selection can lead to local adaptation and genetic differentiation between populations. Ecologists have studied local adaptation

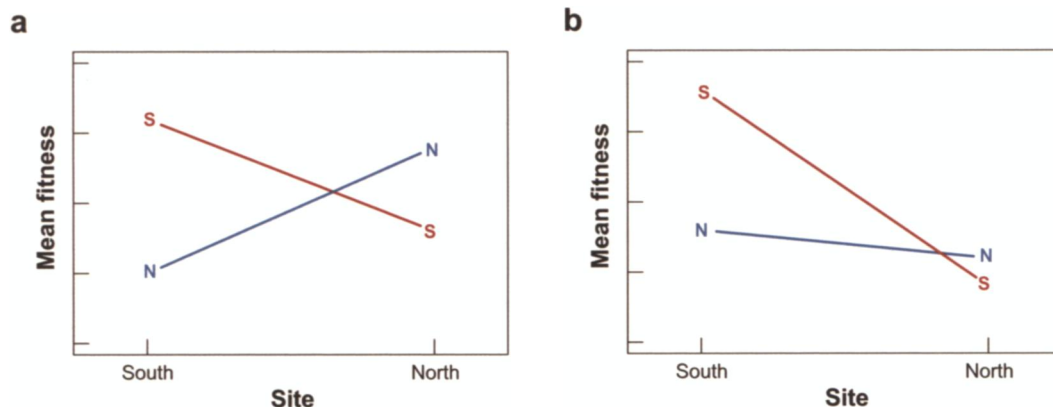


Figure 1

The definition of local adaptation (Kawecki & Ebert 2004). The fitnesses of the northern and southern populations show a genotype by environment interaction. In (a) each has highest absolute and relative fitness at its local site, in (b) both have highest absolute fitness in the south, but each has highest relative fitness at its local site.

in reciprocal transplant experiments. In a classical study, Clausen et al. (1948) transplanted *Achillea* populations between coastal, mid-altitude, and high elevation sites and measured the fitnesses. In such experiments, if the local population always has higher fitness at its home site than nonlocals transplanted to that site, the populations are locally adapted (**Figure 1**) (see Kawecki & Ebert 2004). A relative fitness estimate of a population (when away from its local site) is obtained from a comparison with the local population. For the two examples in **Figure 1**, each population has a relative fitness of 1 at home, and lower fitness elsewhere. This same approach can be used in a continuously varying environment. Notice that in **Figure 1b**, both populations have higher absolute fitness in the south than in the north, but each has the highest relative fitness at home.

Population geneticists examine the conditions in which spatially varying selection can give rise to genetic differentiation and local adaptation. Hedrick (2006) recently reviewed selection in heterogeneous environments at single loci. Many traits related to adaptation have a polygenic basis. The conditions for the maintenance of polygenic variation in an environment that consists of distinct patches depend on the variation of allelic effects over environments (Barton & Turelli 1989).

For forest trees, the most relevant models deal with polygenic traits in a continuously changing environment (Barton 1999, Endler 1977, Slatkin 1978). Genetic differentiation depends on the scale of environmental heterogeneity and the balance of selection and gene flow. In these models, gene action is additive, there are no environmental effects on the phenotype, and selection is weak relative to genetic variation within populations. A one-dimensional axis describes spatial location. For forest trees, the axis may be from south to north and its scale may be in meters or kilometers, to coincide with units of gene flow. Along this axis, the optimum phenotype for some trait varies. For example, the timing of cessation of growth is an important

trait; trees that grow in the north will have an earlier optimum for cessation of growth than those that grow in the south. At each location along the axis, there is a fitness function. The individuals with the optimum phenotype have the highest fitness. As the phenotype deviates from the optimum, the fitness declines. This is described by a Gaussian fitness function

$$W(z) \propto e^{-\frac{1}{2}s(z-z_0)^2},$$

where z is the phenotypic measure of the individual, $W(z)$ is the fitness of an individual with phenotype z , z_0 is the optimum at that location (different between locations), and s describes the strength of selection. A small value of s results in a wide fitness function and weak selection, and a larger s results in stronger selection. Gene flow by gametes follows a symmetric dispersal function, centered on the location of the offspring, with variance σ^2 .

Slatkin (1978) showed that a population's ability to track the phenotypic optimum, i.e., to adapt to the different environmental conditions, depends on $\sigma/\sqrt{(V_A s)}$, where V_A is the additive genetic variance of the trait at each location, and σ and s are as described above. Thus, if dispersal distances are short and selection is considerable, adaptation to a fine-scaled environment is possible. If dispersal distances are long and selection is weak, genetic differentiation is not possible.

The results of this kind of model depend on assumptions about weak diversifying selection. In this case, the mean can change owing to sequential narrow allelic frequency clines at individual loci, where each locus has a high level of polymorphism over a short geographical range (Barton 1999).

With a linearly changing optimum and additional assumptions, the mean phenotype of the population at each site will be at the optimum (Felsenstein 1977). However, if densities are heterogeneous, dispersal is asymmetric, the environmental gradient is not linear, or genes do not contribute additively, the population will not match the optimum exactly (Barton 1999, Lenormand 2002).

Instead of a purely analytical approach as described in the models above, Latta (1998) and LeCorre & Kremer (2003) used simulations with varying optima to examine the effects of differential phenotypic selection on the underlying loci. The simulations were based on a different model of migration, the island model, where each subpopulation is of equal size and receives a constant proportion of migrants from the other populations. Their parameter space includes a wide range of intensities of stabilizing selection within populations, partly outside the range of the model used by Slatkin (1978). With strong diversifying selection and high gene flow, phenotypic differentiation can be due to small allelic frequency changes between populations. Under a rather weak intensity of stabilizing selection within populations, there will be a great deal of linkage disequilibrium (correlations between loci) at the between-population level (Latta 1998, LeCorre & Kremer 2003). Pronounced phenotypic differentiation requires a stronger intensity of selection within populations than is considered by Slatkin (1978). In this case, there is more differentiation at the individual loci and weaker linkage disequilibrium between populations.

Quantitative genetic models assume large population sizes and deterministic spatially varying selection. In small populations, factors such as genetic drift may prevent

genetic differentiation and local adaptation. Extensive gene flow from adjacent areas may prevent a population from tracking the optimum (García-Ramos & Kirkpatrick 1997). Temporally varying selection may prevent spatial genetic differentiation, and one phenotypically plastic genotype might evolve (see Hedrick 2006). Further, populations may not yet be at equilibrium.

In summary, the analytical models are realistic in their assumptions concerning isolation-by-distance and spatially varying selection pressure, but allow only weak selection and symmetric normally distributed migration. The island model simulations allow stronger stabilizing selection, but are based on an unrealistic migration model. Clearly, more realistic assumptions should be incorporated into analytical and simulation models. Further, many parameters of the models need empirical data.

THE QUANTIFICATION OF GENE FLOW THROUGH SEEDS AND POLLEN

Before we address selection, it is important to consider the level of gene flow. Compared with herbaceous and annual plants, trees have more extensive gene flow (Hamrick et al. 1992). Gene flow occurs through pollen dispersal, seed dispersal, and establishment of fertile adult trees. Thus, in addition to dispersal, realized gene flow requires successful fertilization, germination, and survival from competition. Early studies used marking or labeling methods for migration estimation (Koski 1970), but we discuss mainly genetic methods, because they come closer to a description of realized gene flow.

On the basis of the differentiation of maternally (mitochondrial DNA or mtDNA), paternally (chloroplast DNA or cpDNA in some gymnosperms), and biparentally inherited (nuclear DNA) genetic markers, gene flow through pollen is more extensive (20 to nearly 200 times higher) than gene flow through seeds, at least in wind-pollinated trees (Ennos 1994). Highly variable genetic markers allow the determination of paternity and thus the estimation of pollinator-offspring distances. Paternity assignment or exclusion methods measure only current dispersal and ignore establishment. Differentiation among the pollen pools of two or several mother trees can be used to estimate the mean pollination distance and the effective number of pollinators (TwoGener method) (Smouse et al. 2001). These two approaches measure different aspects of pollen flow. For example, the mean distances of pollen dispersal, δ , are similar in *Pinus sylvestris* compared with *Quercus alba* and *Quercus lobata* (Sork et al. 2002), but the effective number of pollinators (pollen donors) is much higher for *P. sylvestris* (Table 1).

Long-distance pollen flow can be extensive (see table 2 in Petit & Hampe 2006). For example, in an isolated *Pinus sylvestris* population in Spain, 4.3% of fertilizing pollen came from a distance of at least 30 km (Robledo-Arnuncio & Gil 2005). Estimates of δ vary between species (Table 1), but are generally hundreds of meters, for both animal (*Dinizia*, *Sorbus*) and wind-pollinated species. To relate these estimates to the polygenic model of spatially varying selection, if dispersal is normally distributed, then $\delta = \sqrt{(2/\pi)\sigma}$. The estimated pollen dispersal kernel functions and shapes vary, but researchers often use an exponential power distribution (Oddou-Muratorio et al.

Table 1 Pollen dispersal estimates of trees, and the methods used for the estimation

Species	N _a ^a	N _o ^b	Dispersal distribution ^c	Method	δ ^d	N _{ep} ^e	Reference
<i>Dinizia excelsa</i>	24	596	Exponential power, b = 0.821	TwoGener, modified	225		Austerlitz et al. (2004)
<i>Fraxinus manschurica</i>	150	492	Two component model	Paternity	197		Goto et al. (2006)
<i>Pinus sylvestris</i>	34	813	Exponential power, b = 0.67	Paternity	136		Robledo-Arnuncio & Gil (2005)
<i>Pinus sylvestris</i>	60	720	Normal	TwoGener	17–29	71–125	Robledo-Arnuncio et al. (2004)
<i>Quercus alba</i>	54	1586	Negative exponential	TwoGener	17	8.2	Smouse et al. (2001)
<i>Quercus lobata</i>	21	211	Normal	TwoGener	65	3.7	Sork et al. (2002)
<i>Quercus lobata</i>	33	288	Exponential power, b = 0.847	TwoGener, modified	121		Austerlitz et al. (2004)
<i>Quercus petraea</i> , <i>Quercus robur</i>	296	984	Negative exponential for short and uniform for long distances	Paternity	287, 333		Streiff et al. (1999)
<i>Sorbus torminalis</i>	60	1728	Exponential power, b = 0.21–0.33	Paternity	743–1077		Oddou-Muratorio et al. (2005)
<i>Sorbus torminalis</i>	60	1728	Exponential power, b = 0.285–0.565	TwoGener, modified	209–482	7–12	Austerlitz et al. (2004)

^aNumber of sampled adults.^bNumber of sampled offspring.^cb = shape parameter.^dAverage distance of pollen flow (m).^eEffective number of pollinators.

2005, Robledo-Arnuncio et al. 2004, Streiff et al. 1999) (Table 1). Distributions are typically fat tailed: More extreme values have a higher probability than in the normal distribution (Table 1), indicated by the estimates of the exponential shape parameter *b*, which are typically between 0 and 1 (Table 1).

Pollen fossil and macrofossil evidence have provided estimates of seed migration rates over long time spans. In Europe, the ice-free areas were quickly colonized as continental ice retreated over the past 18,000 years. Palynological data for most tree species show migration rates of 50–500 m/year, and 1500 m/year for pines (Hewitt 1999). Marker gene-based estimates of average seed flow are not as extensive as pollen flow (however, see Bacles et al. 2006). In *Pinus pinaster*, researchers estimated the average seed dispersal distance to be ~12 m, 40–60 m for *Jacaranda copaia* (Jones et al. 2005), 14 m for *Quercus pyrenaica*, 42 m for *Quercus petraea* (Valbuena-Carabana et al. 2005), and ~540 m for *Fraxinus manschurica* var. *japonica* (Goto et al. 2006). Most genetic and trapping-based direct estimates of seed dispersal are lower than those from fossil data. Genetic and trapping methods may miss some long-distance

migration, and establishment was probably more successful in the postglacial open landscapes (Clark 1998).

Methods that measure potential seed flow may underestimate the relative amount of realized long-distance gene flow. In the immediate surroundings of the mother tree, establishment success increases with distance from the mother tree (Nathan & Casagrandi 2004). For example, in *Pinus pinaster*, estimated seed dispersal distance is higher for saplings than for seeds (González-Martínez et al. 2006). However, the direct measurement of realized gene flow is difficult in long-lived forest trees.

In contrast, indirect methods based on a population genetic model measure realized gene flow over long time periods. In an island model, the differentiation of populations is described by Wright's F_{ST} statistics (see Whitlock & McCauley 1999). Briefly, Wright's F_{ST} statistics assess the proportion of genetic variation found between subpopulations. At equilibrium, migration (m) and differentiation are related to each other as follows: $Nm = 1 - (F_{ST})/4F_{ST}$. Most forest tree species have estimated F_{ST} smaller than 0.1, which suggests extensive gene flow (Slavov et al. 2004). F_{ST} can be used to estimate the relationship between seed and pollen flow (Ennos 1994). However, forest tree populations deviate in several ways from the assumptions of Wright's island model, and gene flow estimates based on F_{ST} should be interpreted with caution (Whitlock & McCauley 1999). First, long-lived trees may only rarely reach the equilibrium assumed and the distribution of genetic diversity may be mostly influenced by population history and demography, not by current gene flow (Austerlitz et al. 2000). Second, in continuous populations the isolation-by-distance model is more appropriate because genetic differentiation and geographical distance are positively correlated (Wright 1943).

With the isolation-by-distance model, pairwise differentiation between subpopulations is used to estimate gene dispersal relative to effective population density by examination of the relationship of $F_{ST}/(1 - F_{ST})$ with geographical distance (Rousset 1997). For instance, Hardy et al. (2006) performed a small spatial scale study and found the gene dispersal distances in 10 tropical tree species ranged from 150–1200 m.

Many studies indicate the existence of long-distance dispersal of pollen and seed (see Petit & Hampe 2006 for examples). These rare dispersal events are difficult to observe, but can have a strong impact on population structure and adaptation (Nathan 2006). A two-component model that separates short- and long-distance dispersal yields the best fit for many data, both for seed and pollen dispersal (Goto et al. 2006, Jones et al. 2005). Estimation of the long tail of the distribution is difficult and heavily model dependent (Austerlitz et al. 2004, Jones et al. 2005). In summary, gene flow extends at least hundreds of meters, but long-range dispersal is poorly quantified. Widely distributed northern conifers and other wind-pollinated trees may spread a part of their pollen even further.

EVIDENCE OF LOCAL ADAPTATION FROM PROVENANCE TRIAL EXPERIMENTS

The study of local adaptation, as described in **Figure 1**, requires that experiments fulfill the following conditions: First, the experimental sites must include

the home sites of the populations. Second, the performance of transferred populations should be compared with the performance of local populations to obtain measures of relative fitness. Third, the traits compared must be reasonable surrogates for fitness.

For close to 200 years, foresters have been transferring seeds and seedlings from different provenances to common garden experiments outside the original location, often in multiple sites (de Vilmorin 1862, Langlet 1971). These experiments provide extensive information on the transfer responses of different populations and species. The main interest of foresters in these studies is to find the most productive (best growing) seed sources for each area, and the experiments serve this purpose well. We summarize some general patterns, and examine whether these studies fulfill the above requirements for the study of local adaptation.

Many forest trees have large ranges over a broad span of environments. For instance, the distribution of *Pinus contorta* spans 33° of latitude and 3900 m of altitude. *P. contorta* grows in areas where the average annual temperature ranges from -7°C to 11°C (Rehfeldt et al. 1999). Trees of individual populations of most species can survive and grow in a broad range of environments, even far from their original growing site, when planted in well tended trials without competition (Eriksson et al. 1980, Heikinheimo 1949). *P. contorta* can maintain good height growth (80% of maximum) in an area where the mean annual temperature spans 6°C (Rehfeldt et al. 1999). In *Fraxinus americanus* plantations in the eastern US, 80% of maximum growth is found 3–5° of latitude north or south from the latitude of origin (Roberds et al. 1990). In *Pinus sylvestris*, for populations between 50°N and 60°N, optimum survival is at a mean annual temperature of 2.7°C, but close to optimum survival is found in areas with mean annual temperatures between 1°C and 5°C (range 4°C) (Rehfeldt et al. 2003). The same study found that several *Larix* species have even broader niches for survival, from 4.6°C to close to 10°C.

Survival and growth may improve away from the home location. For northern parts of the range of *Pinus* and *Larix*, growth and survival can increase by more than 30% when transferred to a location 5° of latitude south, for example (Rehfeldt et al. 1999, 2002, Shutyaev & Giertych 1997, 2000). In contrast, Carter (1996) showed that eight of ten studied tree species in the eastern US would grow better in a cooler climate, with the optimum located north of their current sites. Thus, species and populations from different areas show variable responses.

Even if trees of an individual population can grow and survive in a broad set of climate conditions, the distribution of genotypes changes over much shorter distances. Differences in quantitative traits can be detected between populations that are separated by one degree of latitude (see next section). The distribution of genotypes is governed by relative performance and many biotic interactions.

Analyses of provenance trials rarely aim to address directly the issue of local adaptation. If results are standardized, the comparisons are made against the mean of all provenances at a site, or perhaps the best provenance. In one rare exception, Prescher (1986) analyzed volume production with a comparison of transferred provenances of *Pinus sylvestris* to the local populations to obtain a relative measure of productivity that is closely related to local adaptation. Wu & Ying (2004) compared the height

growth of the local population and a predicted best population to study local optimality. Across part of the range, local populations did have the best growth, but in the west and at high elevations this was not the case.

We used data from a transfer trial series of *Pinus sylvestris* to assess local adaptation with a comparison of the fitness of transferred populations to local populations (T. Knürr, K. Kärkkäinen, and O. Savolainen, manuscript in preparation). The trial was established between 1952 and 1954 by Eiche (1966), and involved a total of 69 provenances transferred to 21 experimental sites in central and northern Sweden that encompass different latitudes (60–68°N) and altitudes (5–765 m). The number of provenances tested per site was either 7 or 14. Provenances were represented by 260 trees for each transfer. Full fitness data are unavailable, but because mortality up to age 20 describes the climate-related mortality (Persson 1994), and height is a good fitness surrogate (Wu & Ying 2004), we use provenance survival rates and mean height 9–12 years after planting for fitness components (Eiche 1966). Tall trees may have good competitive ability, they are healthy, and they will probably have good reproductive success. The two components at least partly comprise different aspects of fitness.

Transfer response functions in relation to latitudinal transfers were first obtained separately for the two fitness components, following earlier studies (Eriksson et al. 1980, Prescher 1986). These curves show the predicted height or survival for the population as it is transferred over latitudes. The response curve for survival of two populations, both from an altitude of 200 m, that originated from latitude 60°N and 66°N, respectively, as well as the survival of the corresponding local populations from the same altitude, are displayed in **Figure 2a**. Relative measures for survival are obtained by dividing the survival of the transferred population by the survival of the local population at each site. Relative measures for the height component were calculated analogously (**Figure 2b**). Multiplication of the two components yields the estimate of total fitness of the population, as a function of the latitudinal transfer distance (**Figure 2c**).

These two examples show several results. The survival and height of local populations are lower in the north than in the south, as was found earlier by Eriksson and coworkers (1980). For the population from the central part of the range (60°N), the highest fitness is at its home site. Close to the northern margin (66°N), the local population is not at the fitness optimum. The local population would have higher relative fitness slightly to the south of its location (**Figure 2c, right**), although its relative height increases when transferred slightly to the north (**Figure 2b, right**). The analysis of relative fitness consisting of two components suggests that populations may be locally adapted in central parts of the range, but local adaptation in *Pinus sylvestris* (in northern Europe) may break down close to the margin of the species distribution.

It is clearly important to consider both components of fitness, because they give somewhat opposing results. The change of environment seems to be more rapid in the north; the fitness of a population (at 66°N) transferred north falls off more rapidly than if it is transferred to the south, as shown by the asymmetric fitness curves. The importance of the two fitness components is different: In the north,

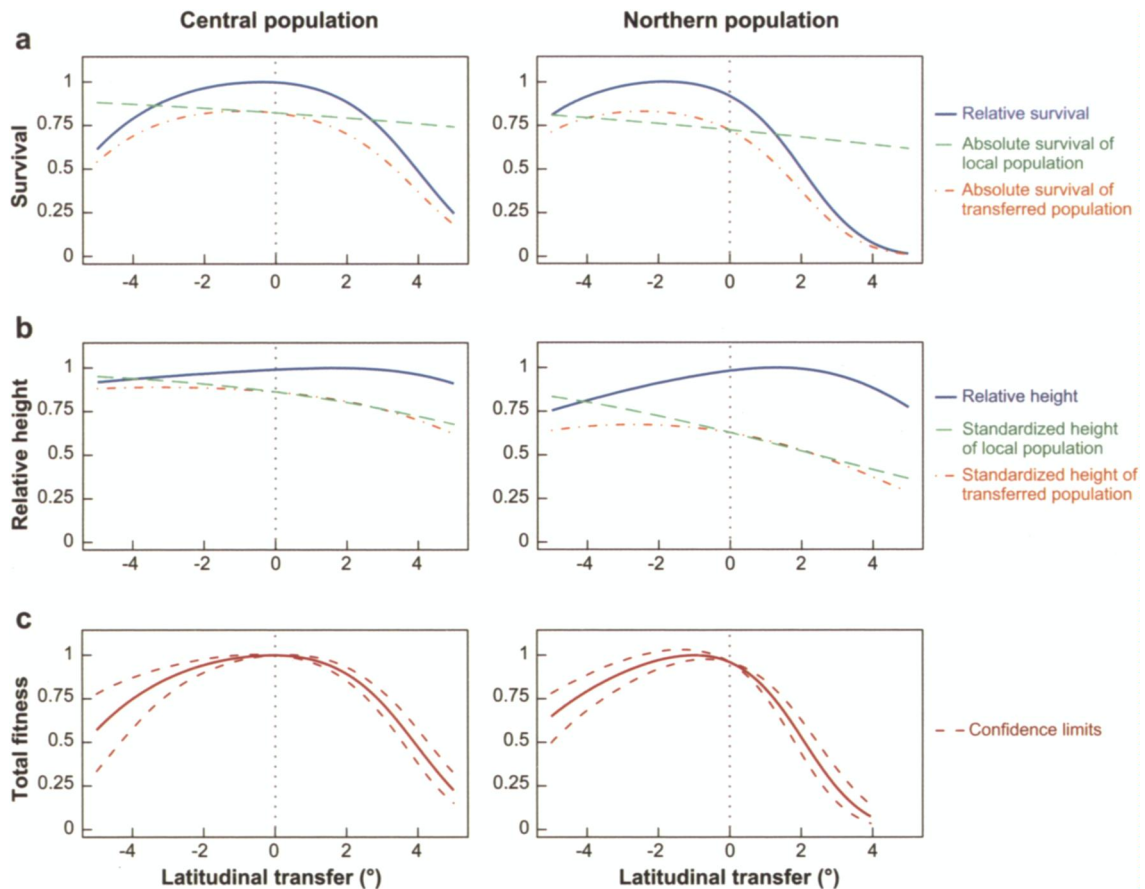


Figure 2

Transfer response functions for fitness and its components in *Pinus sylvestris* for a central population from latitude 60°N and a northern population from latitude 66°N. The bold lines show response functions that relate transferred populations to local populations. Positive numbers indicate latitudinal transfer to the north. Latitudes of local populations are the latitudes to which the central and northern populations were transferred. (a) Absolute survival of the transferred population is indicated by the dashed-dotted line; the dashed line corresponds to absolute survival of the local populations. (b) The dashed-dotted line and the dotted line show standardized heights of the transferred population and the corresponding local populations, respectively; i.e., the heights are calculated as proportions of the maximal height observed across all experimental sites and all provenances. (c) The dashed lines show upper (97.5%) and lower (2.5%) confidence limits of the fitness functions.

the differences between populations are larger in survival than in height growth and competitive ability. The importance of different fitness components differs in transplant experiments that involve herbaceous plants as well (Angert & Schemske 2005).

QUANTITATIVE TRAIT GENETIC DIFFERENTIATION IN ADAPTIVE TRAITS

Here we examine clinal variation in trees in relation to the polygenic models. In the simplest models, the population mean tracks the optimum if the environment changes at a scale less than $\sigma/\sqrt{(V_{As})}$ (Slatkin 1978). The models deal with the distribution of genetic variation after fertilization and before selection. Greenhouses, gardens, or very young trials provide the most appropriate measurements.

The growing season in northern (or very southern) areas is shorter than the growing season close to the equator. The decrease in growing season follows a regular latitudinal pattern in some parts of northern Europe, where longitudinal and altitudinal effects are weak. Many phenotypic traits related to climatic adaptation in northern and central European trees show clines over latitude (**Figure 3**). *Quercus petraea* populations from different latitudes differ with respect to spring bud flush date in a common garden (Ducousso et al. 1996) (**Figure 3a**). *Betula pendula* populations stop growth at different times and day lengths (Viherä-Aarnio et al. 2005) (**Figure 3b**). *Pinus sylvestris* populations set their first year terminal buds in the greenhouse at different times (**Figure 3c**) (García-Gil et al. 2003, Mikola 1982, Notivol et al. 2007), and also display latitudinal clines in cold tolerance (Aho 1994, Hurme et al. 1997). *Picea abies* populations from different latitudes (at altitude 200 m) show different critical night lengths for growth cessation in controlled conditions (Dormling 1979) (**Figure 3d**) or shoot elongation in field trials (Skrøppa & Magnussen 1993).

The examples in Figure 3 were chosen from areas where latitudinal clines are steep. Longitudinal clines also exist, e.g., in cold tolerance for *Pinus sylvestris* (Andersson & Fedorkov 2004). The cline in bud phenology of *Quercus petraea* has an altitudinal component in addition to a latitudinal one (Ducousso et al. 1996). Forest trees in North American mountainous areas, such as *Pseudotsuga menziesii* var. *glauca*, show highly complex patterns of variation that can be accounted for by latitude, longitude, altitude, and slope (Rehfeldt 1989).

In some species, only weak quantitative trait differentiation is found in relation to climate. The clines of *Larix occidentalis* have much gentler slopes than *Pseudotsuga menziesii* or *Pinus contorta* (Rehfeldt 1995), such that genetic differentiation in *Larix occidentalis* is found only with altitudinal differences of 500 m or more. *Prosopis chilensis* provenances over ten degrees of latitude do not vary in frost tolerance (Verzino et al. 2003).

Overall, steep clines may be common where natural selection acts on large populations. Many *Drosophila* species exhibit steep clines across latitudes in traits related to the timing of reproduction (Lankinen 1986). In isolated populations, genetic drift and founder effects may have more influence. For instance, the latitudinal component accounts for much less of the between-population adaptive variation in the weedy annual *Arabidopsis thaliana* than in populations of trees (Stenøien et al. 2002, Stinchcombe et al. 2004).

Spatially varying selection is probably responsible for the patterns seen in **Figure 3**. In principle, genetic drift and isolation-by-distance can also produce these kinds of patterns in neutral traits. However, the tree species represented in **Figure 3**

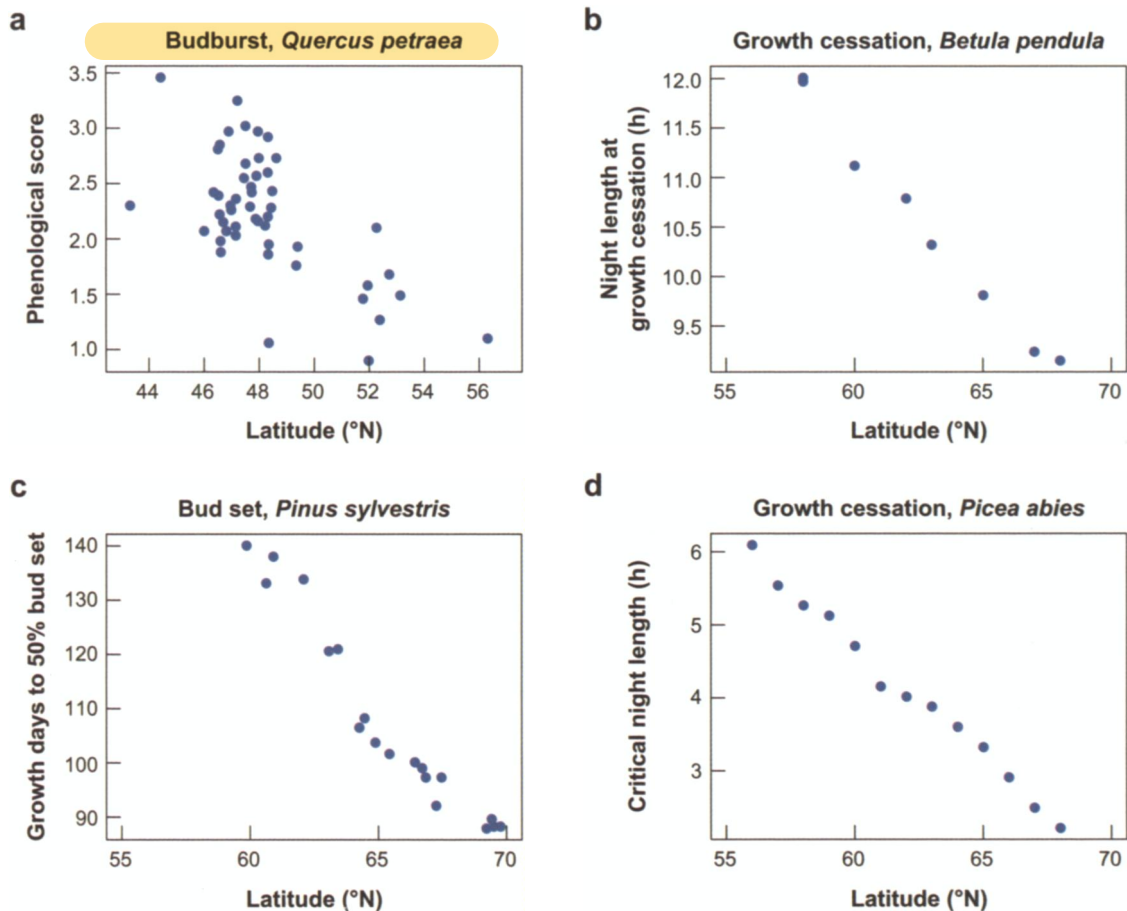


Figure 3

Clinal variation in traits related to timing of growth is shown, redrawn from data from (a) Ducousso et al. (1996), (b) Viherä-Aarnio et al. (2005), (c) Mikola (1982), (d) Dormling (1979). Note that the traits are different, and the latitude scale is not the same in all figures.

[and many other species (Hamrick et al. 1992)] have low differentiation among populations at marker loci (Karhu et al. 1996, Kremer et al. 1997, Lagercrantz & Ryman 1990), which supports the role of selection.

The most commonly used method to assess the role of selection is based on the island model. The measure F_{ST} (proportion of variation between populations at marker loci) is compared with Q_{ST} , an analogous measure for quantitative traits (Prout & Barker 1993). The latter is defined as $Q_{ST} = V_B / (V_B + 2V_A)$, where V_B is the between-population variance (assumed to be all-additive) and V_A the within-population additive genetic variance. If morphological or other polygenic traits show higher differentiation than neutral markers ($Q_{ST} > F_{ST}$), researchers conclude that divergent selection is responsible (McKay & Latta 2002, Yang et al. 1996).

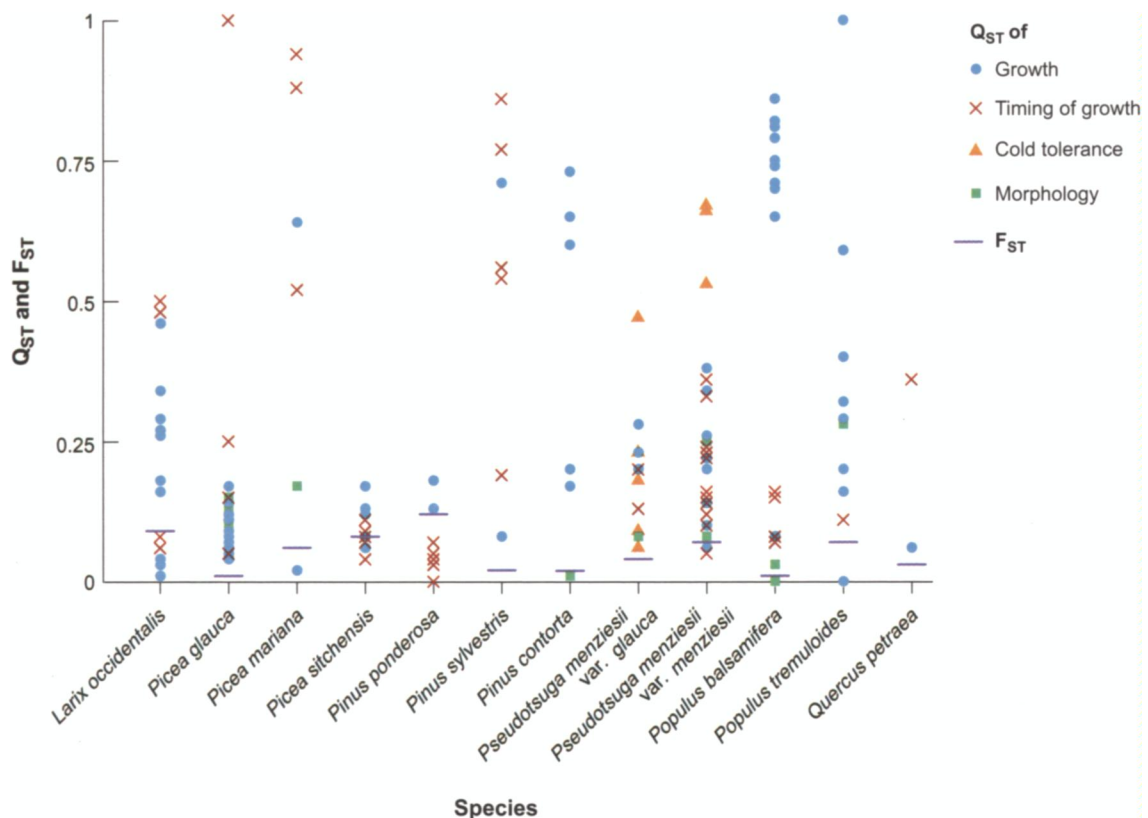


Figure 4

F_{ST} and Q_{ST} values of twelve tree species. For each species, Q_{ST} s of various traits related to morphology (squares), growth (circles), timing of growth (crosses), and cold tolerance (triangles) are presented. F_{ST} s are indicated by horizontal bars. Data are taken from the studies listed in an extensive table available online. See the Supplemental Material link in the online version of this article or at <http://www.annualreviews.org/>.

In **Figure 4**, we summarize the F_{ST} and Q_{ST} information for many forest trees [table 1 of Howe et al. (2003) and additional studies; for the full list of references for **Figure 4**, see the Supplemental Material link in the online version of this article or at <http://www.annualreviews.org/>]. The traits are related to morphology, growth, timing of growth, and cold tolerance. The F_{ST} estimates (horizontal bars) are low for all species. Most of the Q_{ST} estimates are higher, which suggests that the quantitative traits are subject to diversifying selection. The comparison of Q_{ST} estimates between traits, species, and studies is more complicated. The estimates of Q_{ST} are highly dependent on the geographical range of sampling and the number of populations within the range. For instance, the estimates of Q_{ST} for Scots pine bud set differ between studies, depending on the range and number of populations. The very low Q_{ST} estimates for Sitka spruce are based on a large number of populations from a

single island, which constitutes only a very restricted part of the range. In a new study over the whole range from Alaska to California, Q_{ST} estimates were much higher (values not shown in **Figure 4**) for the same traits related to timing of growth (Mimura & Aitken 2007). Regressions of population trait means on distance in this study are more informative than the island model-based Q_{ST} statistic.

The assessment of the role of different factors that govern the clines is difficult in light of the theory on spatial variation in polygenic traits, because we do not have information on the critical parameters (dispersal distance, strength of selection, and level of additive genetic variation). Long-range dispersal is poorly known. Direct measures of the strength of selection are not available for these large-scale clines [as opposed to many smaller scale studies, see Endler (1977)]. However, additive genetic variances along the cline can be estimated (Notivol et al. 2007). A further complication is that the population means may not track the optima (Barton 1999, Felsenstein 1977). Nonadditive modes of gene action and genetic drift can have a role in the clines, but they are not included in the models.

The cases where there is a difference in clinal variation between species or areas can be informative. In a common garden comparison of populations from different altitudes (600–1800 m), *Abies lasiocarpa* showed a steep cline in height at growth cessation, whereas *Pinus contorta* and *Picea glauca* \times *P. engelmannii* were not differentiated (Green 2005). The difference between species may be due to different dispersal distances, but the rate of the change in optima may also differ between species. If clinal variation is examined within a species, for the same trait, in different environmental situations, the balance of selection and gene flow can be more easily evaluated. Frost tolerance in *Pinus sylvestris* varied over latitudes in Sweden (Sundblad & Andersson 1995), but in the same experiment, there was no differentiation between populations covering a similar range of climatic conditions across altitudes, from about the same latitude. The dispersal distances, additive genetic variances, and strength of selection may all be similar in the lowlands and the mountains, but the rate of environmental change per km is much faster in the mountains.

GENETIC ARCHITECTURE AND MOLECULAR NATURE OF GENETICS OF ADAPTATION

Quantitative traits related to adaptation are moderately heritable (Howe et al. 2003). The nature of the underlying genes is still poorly known for most quantitative characters. This information is needed for detailed theoretical predictions on the maintenance of clinal variation. QTL mapping methods estimate the number and location of the loci that govern phenotypic differences between parents of crosses (Mauricio 2001, Tanksley 1993). In trees, mapping is based on existing pedigrees because of the long generation times (Howe et al. 2003).

How many loci are involved in governing variation in a trait and what are the effect sizes? Crosses between *Pseudotsuga menziesii* revealed many (>10) QTLs with relatively small effect (less than 5% of phenotypic variation explained, PVE), related to timing of budset, budflush, and cold tolerance (Jermstad et al. 2001a,b). In *Eucalyptus* and *Salix*, crosses have revealed few (2–5) QTLs for frost tolerance with relatively

large effect (5–15% PVE) (Byrne et al. 1997, Tsarouhas et al. 2004). In *Quercus robur* the variation in budburst was governed by many small QTLs, whereas in the same cross, height variation was due to fewer loci (Scotti-Saintagne et al. 2004). In a cross between a northern and southern Finnish population of *Pinus sylvestris*, some cold tolerance QTLs were found with large effects relative to phenotypic variation within and between populations (Hurme et al. 2000). Likewise, other studies detected QTLs with large effects on cold tolerance in *P. sylvestris* (Yazdani et al. 2003). Recent theory on adaptation suggests that directional selection is initially based on the alleles with largest effects, at least within single populations (Orr 1998). Crosses between closely related species *Populus trichocarpa* and *P. deltoides* measured large QTL effects in cessation of growth (5–20% PVE) (Frewen et al. 2000), not directly comparable to within-species effects.

Variation in different species in similar traits may be controlled by the same underlying loci. A comparative mapping study found QTLs for phenological traits in the same areas of homologous chromosomes in *Quercus petraea* and *Castanea sativa* (Casasoli et al. 2006).

Identification of the actual loci that underly the variation is needed for the examination of the molecular nature of the variation and the effects of individual DNA variants. The improvement in the genomic resources of trees, such as the genome sequence of *Populus trichocarpa*, facilitates this work (Tuskan et al. 2006). The resolution of QTL studies is typically too low to identify individual genes, but studies of sequence variation of candidate loci can provide evidence for the role of a locus (Wright & Gaut 2005). Because forest trees display steep clines of quantitative traits, similar patterns of nucleotide variation may indicate selection. In *Populus tremula*, clinal variation occurs in growth cessation and in single nucleotide polymorphism (SNP) frequency in the phytochrome locus *PhyB2* (Ingvarsson et al. 2006). García-Gil et al. (2003) found no frequency differences in the orthologous locus *PhyP* in *Pinus sylvestris* along a cline in bud set timing.

If the clines in phenotypic traits are due to small frequency differences at many loci, it can be difficult to detect the individual loci (Barton 1999, Latta 1998, LeCorre & Kremer 2003), because linkage disequilibria between populations would be responsible for the change in the mean. So far, few cases of polymorphisms maintained by spatially varying selection have been detected in any species, or any plants in particular (Hedrick 2006, Wright & Gaut 2005). The association of variation of phenotypes with candidate locus genotypes within populations or across clines will provide a powerful method to detect functionally important SNPs in large random mating populations (González-Martínez et al. 2007, Neale & Savolainen 2004). If the effects are small, detection may require very large studies.

SPECIFIC ISSUES AT RANGE MARGINS

When there are no obvious geographical barriers, what limits the spread of a species in constant conditions? Several alternative explanations exist. The populations may lack appropriate genetic variation (Bradshaw & McNeilly 1991), or local adaptation may not have evolved yet after a recent colonization. Finally, gene flow from the more

central parts of distribution may prevent adaptation (García-Ramos & Kirkpatrick 1997).

As an example, we consider *Pinus sylvestris* at its margin in northern Scandinavia, because detailed data on its biology are available. *P. sylvestris* has the widest distribution of all pines, but in northern Europe its distribution ends at approximately latitude 69°N without a geographical barrier. During the ice age, until approximately 10,000 years ago, this area was covered by ice. *P. sylvestris* pollen records show that the species arrived in northern Finland approximately 7000–9000 years BP (Hyvärinen 1975). What limits the distribution of *P. sylvestris* now? Are the northern populations poorly adapted?

As discussed above, a population at latitude 66°N would have had higher relative fitness in a more southern area (T. Knürr, K. Kärkkäinen, and O. Savolainen, manuscript in preparation) (Figure 2c, right). The absolute fitness also declines at the margin. Survival of the local populations is high in warm conditions of 1200 day degrees (d.d., temperature summed for days with average temperature >5°C, which corresponds to approximately latitude 60°N, altitude 200 m), but starts to decrease at about 1000 d.d., and is very low at 600 d.d. (corresponds to approximately latitude 68°N, altitude 400 m) (Persson 1994) (Figure 5a). The northern populations also produce less pollen (and seeds) than more southern populations (Koski & Tallqvist 1978) (Figure 5b). Trees in the north also are less likely to mature their seeds (Harju et al. 1996). The northern populations show ample genetic variation at marker loci (Karhu et al. 1996) and additive genetic variation in quantitative traits, such as timing of bud set or frost tolerance (Savolainen et al. 2004). High mortality and variation between trees in seed production show that directional selection should be possible,

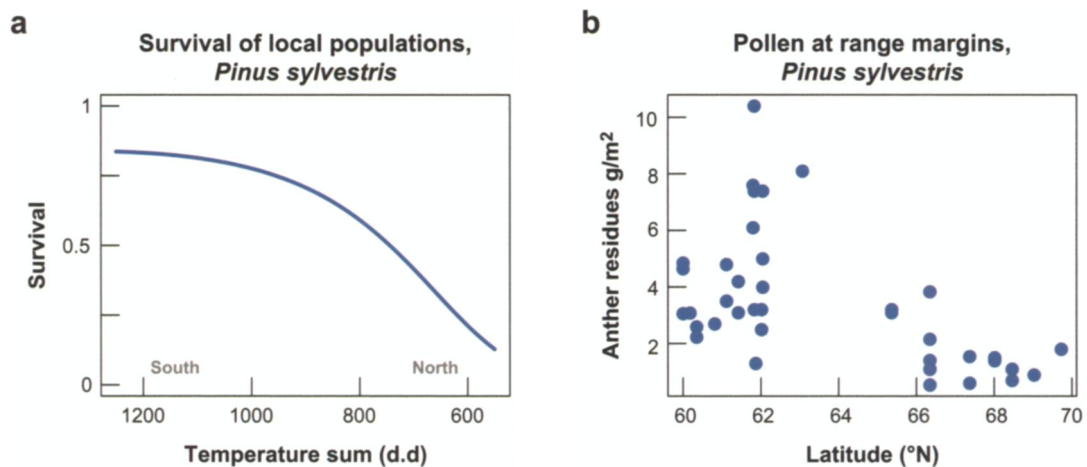


Figure 5

(a) Survival of *Pinus sylvestris* populations to height 2.5 m, as a function of temperature sum in day degrees (d.d), which corresponds to between 60°N at 200 m and 68°N at 400 m, based on data from Persson (1994). (b) Pollen production of *Pinus sylvestris* at different latitudes, based on results presented by Koski & Tallqvist (1978).

and lack of variation does not seem to prevent adaptation. However, the critical traits are often unknown (Hänninen 2006) and may not have been included in these studies.

The hypothesis that asymmetric gene flow from the center prevents adaptation (García-Ramos & Kirkpatrick 1997) can be examined. Pollen production (estimated by counting anther residues) is low at the range margin (Koski & Tallqvist 1978, Sarvas 1962) (**Figure 5b**). The winds from the south that prevail at pollination time bring abundant southern pollen to the northern forests. This nonlocal pollen produces genetic variation, but the progeny are not adapted to these conditions. In experimental crosses, the progeny of north (female) \times south (male) crosses have worse frost tolerance than progeny of north \times north crosses (Aho 1994). Thus, in *Pinus sylvestris* gene flow may indeed have a role in hampering adaptation. Similar effects may take place at other, less intensively studied range margins of tree species.

ADAPTATION TO FUTURE CLIMATE CHANGE

In northernmost Europe, temperatures are expected to rise by about 4°C in the next 100 years (Houghton et al. 2001). Existing trees will show an immediate phenotypic response that will depend on the species and the population. Migration of species and populations to new areas is one possible response (Davis & Shaw 2001), and the ranges of many species are changing already (Parmesan 2006). The potential for local populations to respond by evolving new genotypic composition has also received some attention (Bradshaw & McNeilly 1991, Davis & Shaw 2001, Parmesan 2006). The general theory on polygenic variation suggests that even under strong selection, the response to selection may be slow (Lynch 1996).

Provenance trials are used to predict the immediate responses to a warmer climate. For many northern species (*Pinus sylvestris*, *P. contorta*, and three species of *Larix*), growth is expected to increase in northern parts of the range, but decrease in the southern range margin (Mátyás 1996, Rehfeldt et al. 1999, 2002, 2003). Will trees be able to evolve the new genotypic compositions required for future local adaptation? Rehfeldt and coworkers (2002) made predictions based on experience of selection efficacy in breeding populations. The evolutionary response depends on genetic change by selection in the current population, but the response is also influenced by dispersal. The evolutionary response requires that there are possibilities of establishment for the new seedlings. The high genetic variation of forest trees can facilitate adaptation to new conditions (Hamrick et al. 1992). The evolutionary response can be slowed by limited seed dispersal and reduced possibilities for establishment in the current filled landscapes, in which existing trees survive better than in the earlier, colder climate (Clark et al. 1999, Savolainen et al. 2004). However, the eventual results depend not only on the characteristics of individual species, but also on responses of other competing species (Kellomäki et al. 2001).

CONCLUSIONS

Gene flow in forest trees is extensive, and has given rise in many cases to uniform neutral allele frequencies. The extent of gene flow through pollen is difficult to estimate

because of the long tail of the distribution. In the face of this gene flow, most trees studied show signals of adaptive differentiation in reciprocal transplant experiments or common garden experiments. The strength of selection on the different adaptive traits remains to be quantified. Howe and coworkers (2003) described the quantitative genetics of adaptation at the biometrical level, but studies on the molecular nature of the loci that underly adaptive variation are just beginning. The increasing number of genomic resources for trees will significantly advance these studies, and allow for improved estimates of distributions of allelic effects. Predictions of climate change effects should take evolutionary change into account.

SUMMARY POINTS

1. Foresters have studied adaptation, growth, and survival in forest trees from a forestry perspective extensively, but less often study these issues specifically with respect to the questions of evolutionary biology. For tropical trees, there are few results relating to local adaptation.
2. Gene dispersal estimates of 100–200 m are common for both tropical and temperate trees. This near dispersal can be estimated via the use of genetic markers. The long-distance dispersal may be very important, but it is difficult to estimate.
3. Indirect evidence and the reanalysis of data in an evolutionary perspective show that forest tree populations may be locally adapted over large parts of the range, but at range margins local adaptation may break down.
4. Many forest trees show latitudinal and altitudinal differentiation in adaptive traits, at levels much higher than is observed at neutral genetic markers. This points to strong diversifying selection, but direct estimates of the strength of selection are not available.
5. Current migration of trees is slow relative to climate change. Even if populations have extensive genetic variation, limited dispersal and establishment possibilities may hamper an evolutionary response to climate change.

FUTURE ISSUES

1. Studies of the genetic basis of quantitative variation at the nucleotide level, with sequence analysis and association studies, will help identify the loci that underly quantitative variation. Improved genomic resources will facilitate this work.
2. Soon it will be possible to estimate the distribution of size allelic effects at loci that underly adaptive quantitative variation, and to examine the assumptions of the quantitative genetic models against empirical data.

3. Estimates of selection on quantitative traits in trees and estimates of overall gene flow in trees are needed at the same geographical scale.
4. Much more research is required on adaptation to climate change. Researchers should analyze the potential for evolutionary change in the current ecological context.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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First genome sequence of a tree, which paves the way for genomic approaches in local adaptation research.
