

ADAPTATION OF FOREST TREES TO CLIMATE CHANGE

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Introduction

As the environment changes, trees and other plants can respond in different ways. They may have high phenotypic plasticity and the existing genotypes or populations can simply tolerate the environmental change. Alternatively, they may become extinct due to lack of ability to cope with the abiotic changes. About 10% (8750) of the nearly 100 000 tree species are on the endangered species list, for many different reasons (Oldfield et al. 1998). Further, following changes in the abiotic environment, trees can migrate through seed movement to more suitable areas and thus maintain their 'climatic envelope'. Range extension has been historically a very important way of migration (Bradshaw and McNeilly 1991). Historically, trees have been able to spread fast, largely based on events of long-distance dispersal (Clark 1998). The dispersal rates in general are between 10 and 100 m per year, or a maximum of 100 km per 100 years. These are nevertheless short dis-

tances, compared with what is required by current climate change (Malcolm et al. 2002). Range extension is currently occurring. For instance, the Scots pine (*Pinus sylvestris*) forest limit in northern Finland moved 6 km to the north between 1935 and 1995 (Sirén 1998).

The above-mentioned possibilities have been extensively considered as responses to the current human-induced climate change, but populations may also be able to evolve and genetically adapt to new conditions. This was suggested early by Bradshaw and McNeilly (1991). More recently, Davis and colleagues have examined the potential for evolutionary responses (Lynch 1996; Davis and Shaw 2001; Davis et al. 2005). The genetic structure of many tree populations demonstrates that, in addition to migrating to different areas with changing climate, a common response of tree populations has historically also been to evolve through genetic differentiation

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with respect to the geographically varying climatic conditions. Thus, this possibility deserves attention.

In this paper, we discuss the extent of local genetic adaptation in trees, the evolutionary forces that generate this differentiation, and then evaluate possibilities for trees to adapt to the changing climate, in both natural populations and under silvicultural conditions. We use Scots pine as a special case study, but aim to make some general conclusions on the adaptation of forest trees to climate change. We especially consider northern Europe.

By definition, locally adapted populations have the highest fitness when

compared with other populations at their growing site (Kawecki and Ebert 2004). At other sites, they will have lower fitness than the local populations (Figure 1). Thus, the appropriate test of local adaptation is the ranking (against other populations) of lifetime fitness at the local site. This does not mean that the locally adapted population would not grow better elsewhere, just that they are best at home. This kind of full information is not available for forest trees, but is it needed? Tree breeders are of course not directly interested in this evolutionary definition of local adaptation, because growth and survival in different environments are of more immediate interest. However, it can be important to also consider reproduction or competitive

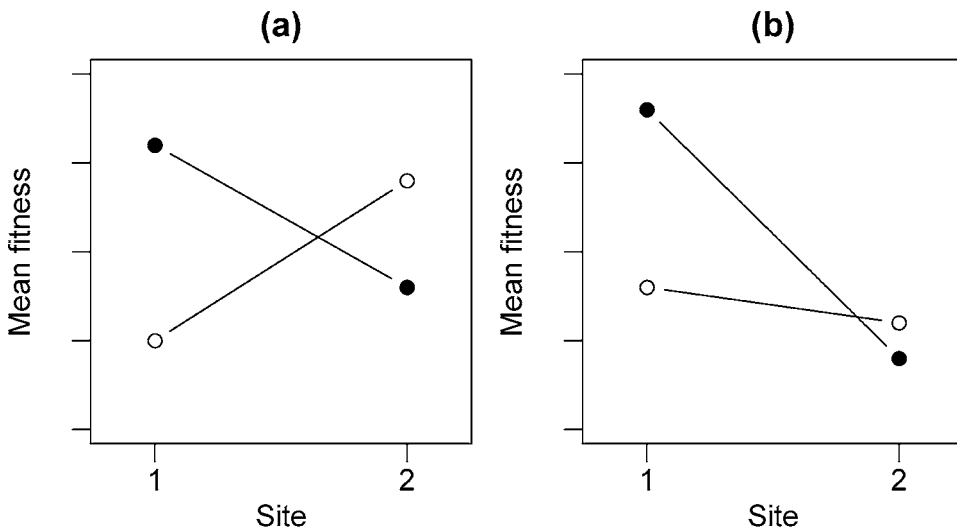


Figure 1. Schematic presentation of local adaptation. Locally adapted populations have higher fitness than other populations at their site of origin. Population A (solid circles) originates from site 1, population B (open circles) from site 2. In Figure 1 (a), each population has highest fitness at its home site; in Figure 1 (b), although population B performs better at site 2, local population A does even better at site 1.

ability in intra- and interspecific competition. During climate change, economically important tree populations may be intensively managed with silviculture to directions decided by humans but other, natural tree populations will follow the rules of natural evolution. Thus it will also be important to understand the evolution of local climatic adaptation and to take both natural and human directed evolution into account.

Trees have evolved through local adaptation: evidence from provenance trials and clines

Results on local adaptation in trees come from two sources: provenance trials and patterns of clinal variation. Provenance trials of forest trees differ from classical local adaptation experiments of other plants in many ways (Clausen et al. 1948). Seedlings are planted as plots of seedlings of the same origin, in spaced plantings, where both intraspecific and interspecific competition are avoided, or at least reduced. Not surprisingly, reproductive fitness is practically never studied in such trials. Thus, two important fitness components, early survival in competitive conditions and reproductive ability, are not included.

Provenance trials are generally not designed to test for local adaptation, but for finding genetic materials that could be used to increase productivity. Eiche (1966) and Eriksson et al. (1980) found in large Scots pine experiments that

seedlings transferred southward [in the northern hemisphere] had increased survival. Beuker (1994) also found that volume production of northern provenances increased upon transfer to the south. The results of a very large Scots pine provenance trial (Shutyaev and Giertych 1997) were used by Rehfeldt et al. (2002) to assess Scots pine response to climate change. Again, northern provenances transferred south to warmer climates had higher growth than at their original location. Thus the northern populations are likely to benefit from the warming climate. However, this large-scale study also predicted that the southernmost populations in the northern hemisphere are likely to suffer from the warming climate. This suggests that the limiting factors of Scots pine populations differ in the different parts of the range. Findings of increased (radial) growth upon climate change in the expected elevated temperatures have also been made in experimental studies (Kilpeläinen et al. 2005).

Note that compared with the above definition, the studies do not address the issue of whether forest trees are locally adapted. The northern populations transferred to the south may grow better than at home, but worse than the southern populations at those sites. But is the local population best in fitness? Wu and Ying (2004) analyzed provenance trial data of Lodgepole pine (*Pinus contorta*). They used height growth as a surrogate for fitness, and found that, in a large

part of the range, the local population was optimal for height growth. The large study of Scots pine also found evidence of local adaptation (Shutyaev and Giertych 1997). Very northern and very southern materials in the northern hemisphere were not found silviculturally interesting, because they were inferior in growth performance to those from more central latitudes, except locally. This finding of local superiority is evidence of local adaptation. Thus, even when just using height as a fitness surrogate, provenance trials do show evidence of local adaptation.

We also know that Scots pine has limits to its adaptation. In northern Scandinavia, the distribution range ends without any geographical barrier. While survival is high in areas of temperature sums of more than 800 day degrees, in colder areas (e.g. northern Sweden, about 67°N at low altitudes) survival rapidly decreases (Eiche 1966). Likewise, northern populations in areas with temperature sums less than 1000 day degrees show poor adaptation in terms of seed maturation (Harju et al. 1996). Thus, it seems the populations may not be able to fully adapt to the severe conditions. The existence of genetically determined clinal variation in adaptive traits along environmental gradients is also evidence of local adaptation, especially if neutral markers in the genome show no corresponding differentiation (Prout and Barker 1993; Merilä and Crnokrak 2001; McKay and

Latta 2002). Evidence of such clines is abundant in forest trees. For instance, in common garden experiments in the northern hemisphere, Scots pines of northern origin set their terminal buds before the southern ones (Mikola 1982; Hurme et al. 1997; García-Gil et al. 2003). Figure 2 shows an example of such a cline over the Scandinavian latitudinal range for timing of bud set of one-year-old Scots pine seedling, grown in common garden conditions (as described earlier, e.g. by García-Gil et al. (2003)). In the same range, the divergence at neutral markers is much lower (Karhu et al. 1996; García-Gil et al. 2003). Similar variation patterns that are concordant with climate variation have been found in many forest trees, such as Norway spruce (*Picea abies*) and Lodgepole pine (Lagercrantz and Ryman 1990; Yang et al. 1996). Cold hardiness also shows such patterns of variation in Scots pine (Aho 1994; Hurme et al. 1997) and in many North American conifers (as reviewed by Howe et al. 2003). In sessile oak (*Quercus petraea*), there is a longitudinal cline in timing of bud flush (Kremer et al. 1997). The latitudinal ecotypes of other woody perennials, including species of willows (*Salix* spp.), also show photoperiod-dependent variation in cessation of growth (Junttila 1982). Furthermore, populations of forest tree species show differences in adaptation to drought. In the Mediterranean region, summer drought is a major factor limiting plant distribution and growth. Variability in

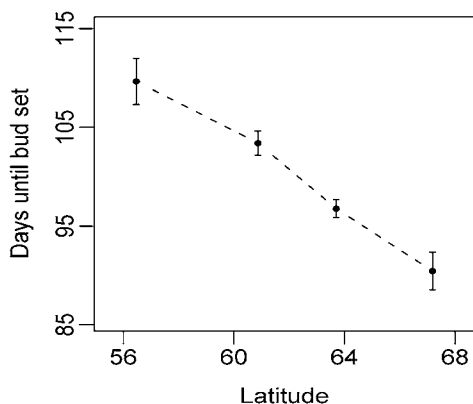


Figure 2. Timing of bud set in first-year seedlings of Scots pine (*Pinus silvestris*) in a common garden environment in the northern hemisphere. Northern populations set their buds much before more southern ones (T. Knürr, K. Kärkkäinen and O. Savolainen, personal communication). For methods, see García-Gil et al. (2003).

ecophysiological response to drought is found among geographical races of maritime pine (*Pinus pinaster*) (Fernandez et al. 1999). Adaptation to different soil water conditions may also be due to structural rather than physiological variation, as was found in Scots pine (Palmroth et al. 1999).

In most of these cases, there is little differentiation at neutral markers. The steepness of the clines and the degree of differentiation depends on the balance between gene flow through seeds and pollen, as well as natural selection (Ennos 1994; Barton 1999). The low differentiation of marker genes reflects high migration rates. In the oak clines, traces of history have been eliminated, as shown by Kremer et al. (2002). In Norway spruce, the quantitative trait

differentiation is partly also reflected at marker genes, suggesting that history is also reflected in patterns of quantitative variation, in addition to selection (Lagercrantz and Ryman 1990).

Potential for adaptation

The genetic response to selection depends on the heritability of the trait and on the intensity of selection. The familiar breeder's equation states that $R = h^2S$, where R is response, h^2 is heritability and S the selection differential. Forest trees are highly variable in most quantitative traits. Much of this variation is genetic, giving rise to moderate and high heritabilities (Cornelius 1994). Specifically, this has also been found to hold true for timing of bud set in Scots pine, where heritabilities in two populations were 0.33 to 0.67 (Savolainen et al. 2004). Also, cold tolerance is found to be heritable, with more variable results, as reviewed by Howe et al. (2003). The real potential for evolutionary response is measured by additive genetic variance. A high heritability does not guarantee an evolutionary response if both additive genetic variance and total phenotypic variance are low (Houle 1992). Selection in tree populations can be strong, as mortality can be high. Thus, there is considerable capacity for high selection differentials. The populations are large, and there is much gene flow, so that genetic drift is expected to be a minor factor. The conditions for a selective response are therefore favourable.

In simple situations that correspond to the model, there can be very rapid genetic change. Introduced plant populations sometimes adapt rapidly to the local climatic conditions. Introduction of exotic tree species or provenances has quickly produced new landraces under the combination effect of natural and artificial selection (Eldridge et al. 1993; Hahl 1978). Large-scale provenance transfers of Douglas fir (*Pseudotsuga menziesii*) to Europe have resulted in locally adapted populations (Kleinschmidt and Bastien 1992). Evolution in natural conditions can also be relatively rapid. Novel photoperiodic genotypes adapted to the very long days of northern Scandinavia evolved in silver birch (*Betula pendula*) during colonization after the last glacial maximum, taking only a few thousand years (Viherä-Aarnio et al. 2005).

Gene flow influences the process of adaptation. When new areas are colonized, seed migration is especially important (Austerlitz et al. 2000). In the later stages, pollen flow is especially effective. This is reflected in the lack of differentiation for most of the genome. Gene flow can hamper adaptation in marginal populations, but it also provides more genetic variability for selection to act upon. These general features of forest trees show that selection is likely to be powerful. This has led some authors to conclude that forest trees will be able to adapt to the current climate change without problems.

Evolving in the changing climate is a complex process

Evolution during the current climate change is a more complicated situation than colonization and adaptation after the ice age. The present environmental changes are taking place rapidly. In northern Europe, temperature is expected to increase by at least 4° to 6°C within the next hundred years (Houghton et al. 2001). The landscape is not empty but filled with existing plant species. This will make colonization of new areas much more difficult for many trees (Malcolm et al. 2002). For some species, such as Scots pine, interspecific competition is predicted to be more intense, as climate change is likely favour other species, such as birch (Kellomäki et al. 2001). Ecologists have thus predicted that Scots pine will decline, while tree breeders have suggested that it will do very well in the northern areas under the warming climate (Kellomäki et al. 2001).

As the biological situation is quite complex, we used simulations to evaluate the potential of trees to adapt genetically to a new environment, through local selection and through gene flow, mostly by pollen (Savolainen et al. 2004). The basic assumption is that the genetic composition of the population, with respect to timing of growth (or cessation of growth), should follow the 'climatic envelope'. The temperature sum at latitude 68°N is expected to be approximately like the temperature sum at latitude

61°N currently. Thus, the population at 68°N should evolve to have the timing of growth characteristics of the population currently found at latitude 61°N.

We simulated adaptation of 10 Scots pine populations equally spaced along a latitudinal climate gradient, all consisting of 1000 individuals that reached maturity at 20 years and a maximum age at 150 years. Vacancies left by individuals that reached the maximum age were filled by the best adapted (see below) of 20 seedlings, the mothers of which were sampled at random from the population where the vacancy occurred, while the fathers were sampled from a randomly sampled population. This reflects that dispersal in Scots pine is mainly by pollen. Paternal populations were sampled from a normal distribution with zero mean and unit variance, which translates into pollen dispersal distances that make the 10 populations correspond approximately to the latitudinal range of Scots pine in Finland.

Contrary to adult trees, seedlings (i.e. individuals younger than 20 years) may die due to frost damage. We assumed that the autumn onset of frost varies linearly from south (late onset, long growing season) to north (early onset, short growing season). Seedlings must set bud (and become frost hardy) before the onset of frost, otherwise they die. Timing of bud set was modelled as a quantitative trait with 50% heritability, governed by 5 additively acting loci on different

chromosomes, with two alleles per locus. Seedlings that set bud after the onset of frost quickly die in the simulations. In contrast, seedlings that set bud too early remain small due to their short period of growth. They are therefore likely to lose the competition for space. We assumed that competition for space takes place dominantly during the seedling stage. Therefore, the 'best' seedling, that fills a vacancy, is the largest of the 20 seedlings that did not die due to frost damage. There is thus a stabilizing selection, with frost selecting against late bud set and competition against early bud set. As the onset of frost varies clinally, so the point towards which selection acts differs clinally between populations.

From random initial genotypes and age distribution, the populations were set to adapt to a stable (but clinally varying) climate for 5000 years. Then climate change began, with the onset of autumn frost changing by equal increments each year and in every population for a period of a hundred years. The magnitude of change is such that the northernmost populations experience the climate of the southernmost after 100 years. That corresponds to the prediction from climate change models that, in a hundred years, northern Finland will have the climate that is currently found in southern Finland. The magnitude of change depends in this way only on the steepness of the initial cline. After 100 years of climate change, the response of the populations was monitored for another

400 years, during which no further climate change took place.

After having grown adapted to a stable, climally varying climate, the simulated Scots pine populations are clearly locally adapted, as population average bud set date closely follows the cline in onset of frost (not shown), with early bud set in the north and late in the south. Climate change evokes a response in the climally adapted Scots pine populations. The change in the mean of the overall populations (including all age classes) is shown in Figure 3. Because adult trees do not die due to frost damage or competition, the response of the populations to changing climate is much slower than the climate change itself. Thus, these simulations that are based on the biology of the species, suggest that the genetic change in Scots pine will be very small

during the next 100 years. In northern Europe, the existing trees will survive for a long period under the warmer climate and there will be few sites available for the new, genetically more adapted seedlings. At the same time, the surviving trees will act as a buffer against an immediate population decline.

Change was achieved through new individuals that enter the population only when vacancies occur, which happens relatively rarely in a long-lived species like Scots pine. Under climate warming, pollen migration from the south can increase the rate of adaptation (within reasonable values). Genetic and phenotypic change of the pine populations still continues after climate change has ceased. Only 500 years after the onset of climate change, that is 400 years after the climate has stopped changing, do

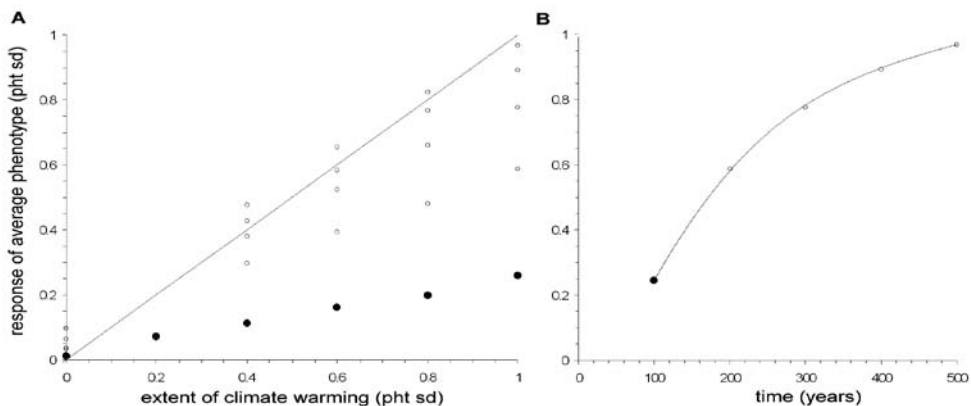


Figure 3. Response of clinal Scots pine (*Pinus silvestris*) populations to climate warming. A. The relation between phenotypic response and intensity of climate change. Climate change and response are measured in phenotypic standard deviations (pht sd). B. Phenotypic response over time when the intensity of climate change is -0.25. For both panels: closed dots represent average change over 10 populations in the average phenotype after 100 years of climate change. Open dots represent the subsequent averages after intervals of 100 years. The straight line in panel A is $x=y$.

phenotypic and genetic change in the populations cease. Interestingly, that period does not depend on the intensity of climate change: if the initial cline is shallow, and consequently climate change is less intensive, the response of populations is also smaller, but it continues about as long. In all simulations, irrespective of the intensity and direction of climate change, it takes approximately 500 years before genotypic and phenotypic response is complete.

Rehfeldt et al. (2002) considered how long it would take for local populations to evolve to a new optimum, using the simple models. They suggested about 13 generations, which in Scots pine could be much longer than the time that we predict here. The difference is at least partly accounted for by considering migration.

Evolution may be slowed down by various factors. Etterson and Shaw (2001) found that negative genetic correlation may slow down the response. Also note that, in our case, migration from the south contributes to speeding the response to climate change. However, the southern populations will not experience any migration from the south, and migration from populations in the north will have the opposite effect, preventing adaptation. Rehfeldt et al. (2002) predicted that some southern populations might become extinct if they are not able to evolve. Lynch (1996) reviewed the theoretical results of quantitative genet-

ics. Initial responses of populations with high genetic variability can be very large for many generations, accompanied by high mortality. However, the long-term sustainable response within individual populations per generation is only a few percent of the phenotypic standard deviation.

Competition between species may have very important effects. In the southern part of the distribution range, the situation may be quite different due to different selective agents (i.e. drought stress instead of adaptation to cold). Sabaté et al. (2002) studied impact of climate change on growth of five forest tree species (*Quercus ilex*, *Pinus halepensis*, *P. pinaster*, *P. sylvestris*, *Fagus sylvatica*) at seven Mediterranean sites representing different environmental conditions, with a broad range of elevation, latitude, rainfall and temperature patterns. The simulations show that increased temperature and rainfall in the region, together with increased atmospheric CO₂, will have positive effects on forest growth and wood production. However, the response of different tree species may differ.

Conclusions and recommendations

The effects of changes in interspecific competition and reproductive potential should be included when considering climate change effects. The adaptation of trees can be aided by appropriate moving of forest reproductive materi-

als, taking into consideration seasonal adaptation. High genetic variability and much opportunity for selection allow natural selection to result in adaptation. Research work on short-lived model species can also help in understanding climate change consequences. The potential changes in the growth rhythm of trees in a changing temperature environment but current photoperiodic conditions need to be examined more closely. More detailed information on the genetic basis of growth rhythm would help us to build more reliable models of possible processes.

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