



Evolutionary Responses of European Oaks to Climate Change

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ABSTRACT

There are widespread concerns that trees, as long-lived species, may not be able to cope with future climate change. Trees experienced large climatic changes over much longer time periods during many previous interglacial periods. The evolutionary trajectories of trees during these periods were reconstructed in this study, in an attempt to predict how trees might respond to future environmental changes caused by climate change. Taking the European oaks as a study case, this review shows that rapid migration and adaptation, extensive gene flow and hybridization were the main processes that permitted oaks to track climatic warming in the past. Future evolutionary trends of oak populations in response to climate change are then considered. The potential for species to migrate via seed dispersal to more favorable locations (e.g., northwards) will be limited. On the other hand, it is likely that natural selection will act on a diverse gene pool (in part due to large population sizes), perhaps allowing local adaptation even if this ultimately reduces diversity. Substantial evolutionary shifts can be expected in a limited number of generations. The high levels of genetic diversity and gene flow from other populations will favor rapid adaptation. However, many tree populations may be tested to the limits of their adaptive potential, so some intervention may be needed. To enhance the adaptive potential of populations, it is recommended that genetic diversity be increased by “mixing” local stock with nonlocal material (seeds or seedlings). Guidelines, providing information on permitted directions and distances for the transfer of reproductive material (seed or seedling), should be developed based on current scientific information, especially on data from existing provenance tests.

Keywords: climate change, environmental response, gene flow, provenance research, hybridization, pollen dispersal

Introduction

There are widespread concerns that trees, as long-lived species, may not be able to cope with future climate change. Trees have experienced large climatic changes over much longer time periods during many previous interglacial periods. Although the rates of environmental change were lower than what is now occurring in response to climate change, the evolutionary mechanisms may be similar. It is therefore of the utmost importance to learn about past evolutionary trajectories to predict future responses.

The genetic and ecological mechanisms that have facilitated adaptation of trees during historical “natural” warming periods, taking European oaks as example species, are reviewed in this paper. Oaks are ideal species for this purpose. The postglacial history of temperate oaks in Europe has been reconstructed in detail by combining genetic and historical approaches (Kremer, 2002). Assembling information and results about the postglacial history and genetics (mainly provenance research) of oaks, this paper shows how oaks have responded rapidly to environmental change in the past, despite their low evolutionary rate at the gene level. Learning from the past, this paper also provides some clues about ongoing and future adaptive responses to climate change.

What have we learned about the evolutionary responses during natural warming?

During the Quaternary period, the earth’s climate was dominated by the succession of more than 15 glacial and interglacial periods. Glacial periods lasted between 70 and 100,000 years, while interglacial periods were much shorter (from 10 to 20,000 years) (Hays et al., 1976). These repeated drastic environmental changes were followed by important alternating retractions and expansions of tree species distribution, placing them in different habitats over time and space. These changes also represented very severe selection filters. Indeed, extinctions of European forest trees occurred between 2.4 and 1.7 million years ago, during the early and severe glacial cycles of the Quaternary.

Fossil evidence shows that many species in the *Fagaceae* family that existed in Europe at the end of the Tertiary have since disappeared and are now only present in North America and/or Asia (e.g., species belonging to *Fagaceae* genera *Lithocarpus*, *Castanopsis* and *Trigonobalanus*). There has been no tree species extinction during the most recent periods, suggesting that extant tree species in Europe have demonstrated an efficient ability to migrate and adapt to environmental change. Quaternary evolutionary history suggests therefore that in the face of drastic environmental changes these species developed mechanisms to help reduce the likelihood of extinction. Recent investigation in evolutionary and population genetics has identified at least four of those mechanisms: rapid migration, extensive gene flow through pollen dispersal, interspecific hybridization, and rapid adaptation.

Rapid migration

The distribution of temperate white oaks in Europe has shifted repeatedly from the Mediterranean to the boreal regions during interglacial and glacial periods. At the end of the last glacial maximum, oak forests were restricted to the Iberian Peninsula, Italy, and the Balkan Peninsula (Greece and the western coast of the Black Sea). A pan-European survey of fossil pollen remains (Brewer et al., 2002) showed that all refugial sites were



1/ *Quercus robur*, Bialowieza Forest, Belarus/Poland.

located in mountainous areas (e.g., Sierra Nevada in Spain, the Southern Apennine chain in Italy, and the Pindos mountains in Greece).

During the postglacial period, between 13,000 and 10,000 BP, oaks increased in abundance in mountainous areas (in the Pyrenees, the southeastern Alps, and the Carpathian mountains). The cooling of temperatures during 11,000 BP to 10,000 BP stopped this expansion and eventually resulted in a decrease in the size of the species' geographical range. After 10,000 BP, oaks spread throughout Europe and reached their current distribution at about 6,000 BP. The expansion was more rapid in the west and was reduced in the center and east due to the Alps and the Carpathian mountains. The velocity of oak migration during the postglacial recolonization period (between 15,000 to 6,000 BP) averaged 500 m/year (Brewer et al., 2002), reaching in some cases up to 1,000 m/year. These figures are much larger than those predicted by migration models based on dispersal agents. However, if rare long-distance dispersal events are included in the models, then the overall expansion rate generated by the aggregation of the many populations that were founded by the long-distance dispersal events may account for these rapid migration rates (Le Corre et al., 1997; Bialozyt et al., 2006).

Extensive gene flow through pollen dispersal

As migration proceeded northwards from the different source populations, the colonization routes merged in Central Europe resulting in genetic homogenization as these different populations interbred. The resulting genetic diversity was so great that the genetic imprint of the original refugia from which they were derived was virtually erased. Pollen-flow dynamics in *Quercus petraea* (Matt.) Liebl. and *Q. robur* L. stands have been studied (Valbuena-Carabana et al., 2005; Streiff et al., 1999). These studies revealed that more than half of the pollen contributing to the next generation came from outside the study stands, with pollen dispersion curves characterized by long “tails”. The results of recent large-scale genetic surveys indicate that the level of genetic diversity at the northern edges of the natural distribution range reach the same levels as in the

refugial glacial areas (Zanetto and Kremer, 1995). This was also most likely the case as migration progressed. The end result of extensive gene flow is the maintenance of genetic diversity even at the migration front, allowing rapid adaptation of the newly colonizing populations.

Interspecific hybridization as a colonization process

Hybridization is common in oaks, but its evolutionary role during recolonization has only recently been investigated. One intriguing result was that hybridization can allow species to migrate via pollen instead of seed (Petit et al., 2003). There is now much evidence that hybridization permitted *Q. petraea* to colonize new sites by hybridizing with *Q. robur*.

The colonization scenario can be described as follows: because *Q. robur* tends to be a more pioneering species than *Q. petraea*, it was present at the northern edge of the oak migration front with *Q. petraea* somewhat behind, but still capable of hybridizing with *Q. robur* through pollen flow. If the first generation hybridization is followed by later backcrosses (e.g., between hybrids and parents) with *Q. petraea* as male parent, then successive introgression would lead to the restoration of *Q. petraea* trees within the *Q. robur* stand. The end result is that *Q. petraea* becomes established within the *Q. robur* stand, consequently enhancing species succession. The peculiar role of hybridization shows that colonization of newly available territories by oaks (for instance following successive ice ages) is facilitated by interspecific gene exchange, allowing some species to bypass colonization by seed to rapidly invade new sites.

Rapid adaptation

After colonizing a new site, the newly established populations begin to differentiate genetically from the source populations from which they were derived. There is now evidence that the genetic divergence among extant populations that can be observed in provenance tests is the result of adaptive evolution due to local selection from the time of establishment of populations on new sites (Kremer et al., 2010). Indeed most phenotypic traits show clinal variation, with different clinal patterns of variation for different traits (Ducouso et al., 2005). There is little evidence in current populations of any phenotypic or adaptive trait differentiation relating to refugial origin, even in neighbouring Central European populations that are known to have originated (through migration) from different refugia. This is interpreted as the result of extensive gene flow during admixture followed by local adaptation (Kremer et al., 2010). One may conclude from these analyses that most variation in provenance tests is the result of recent adaptive evolution.

How will evolutionary processes stimulate adaptive responses under climate change?

The response of natural tree populations to climate changes has been sketched out in three different scenarios: “persistence through migration to track ecological niches spatially, persistence through adaptation to new conditions in current locations, and extirpation.” (Aitken et al., 2008). The actual outcome for oak populations will depend on the interplay between the different evolutionary processes just described. It is important to evaluate how these natural mechanisms are activated in order to determine if human intervention is needed. In the following sections, predictions on the potential impact

of climate change on oak populations based on historical as well as on contemporary records are made.

Seed migration constrained by natural seed dispersion

Predicted future bioclimatic envelopes provide some rough indications on the distance that populations would need to shift to remain under the “same” bioclimatic conditions. In the case of *Q. petraea*, a shift of 200 to 500 km north and northeast by the end of the current century is predicted, depending on the level of greenhouse-gas emission (Thuiller et al., 2005). Under the most severe scenario (gas emission model A1F1; climate model HadCM3) the bioclimatic envelope excludes France, but would cover the southern half of Finland.

Information on seed velocity is available from the postglacial recolonization period and these data can be used to assess the likelihood that oaks will be able to migrate quickly enough in response to the displacement of the envelope. Palynological records indicate migration velocities ranging from 500 to 1,000 m/year, amounting to a displacement of 50 to 100 km in one century. At the most, oaks would be able to shift their range 100 km during the next hundred years, not taking into account the likely negative impact on migration caused by land fragmentation due to agricultural and other land uses. Future migration velocities, in response to climate change, inferred from past migration patterns may not be accurate (where it is assumed that dispersion capacities are the same under different environmental conditions). There is a large gap between the velocity estimates and the actual velocity needed to cope with the shift of the bioclimatic envelope.

Hybridization facilitating migration and succession

While there are only two temperate oak species (*Q. petraea* and *Q. robur*) in Europe, there are more than 20 species and subspecies located in central and Mediterranean areas (*Flora Europaea*, Schwarz, 1964). They belong to two main oak sections (*Cerris* and *Quercus* sensu Nixon) and hybridization within sections is quite common (Curtu et al., 2007; Lepais et al., 2009). Climatic change is expected to cause species migration, with more range overlaps and competition for new niches in the newly invaded sites. This might be expected to increase the opportunities for hybridization and introgression among species. There are two ways in which hybridization may enhance adaptation of oak populations to climate change.

Hybridization will accelerate species migration by repeated unidirectional interspecific crosses with *Q. robur*, just as hybridization permitted *Q. petraea* to migrate northwards during the postglacial period. Similar hybridization events may occur with other species combinations involving Mediterranean oaks, facilitating the establishment of Mediterranean species at more northerly latitudes. Hence hybridization may help overcome the limitations of species migration via seed that was limited to less than 100 km because pollen is dispersed over longer distances than seed.

Hybridization will facilitate establishment and species succession on new sites. Oak species are characterized by strong differences in site preferences. Just as *Q. robur* and *Q. petraea* differ in their water requirements, the Mediterranean oak species have different soil-type preferences. As hybridization will accelerate the migration of species, it will subsequently facilitate their establishment on the most suitable sites of those already occupied by temperate species. In the long run, this process will result in the replacement of one species by another, which in turn may accelerate ecological succession.

Gene flow enhancing adaptation

Local adaptation can be increased by “incoming genes” via pollen from populations



2/ *Quercus petraea*, Kosienice Forest, Poland.

exhibiting higher fitness than the receiving population. In the case of directional environmental changes towards higher temperature, it is likely that populations from more southerly latitudes may be an important source of this pollen (Kremer et al., 2012). The question raised here is whether pollen dispersal distances will be of sufficient magnitude to shift species' bioclimatic envelopes.

Gene flow may contribute to increasing the fitness of a given population that is under severe selective pressures. Migration of alien genes through gene flow will change the genetic composition of the receiving population. If the migrating gene has a positive effect on fitness, it will rapidly increase its frequency in the receiving population. The dynamics of migrating genes (migration rates, subsequent frequency, variation, and change in population fitness) have never been monitored in forest tree populations, but deserve more attention in light of the increasing focus on the impact of climate change. Clearly, a species that has a continuous distribution across contrasting ecological sites might be able to "import" genes contributing to higher fitness in areas exposed to severe stress. Most of these theoretical and experimental studies have shown that gene dispersion has both local and large-distance components, as revealed by the existence of the "fat tails" of the dispersion curve.

The second component is, of course, more relevant in the context of climate change. Sites that are currently considered moist are likely to become drier in the future, so trees growing on these sites would potentially benefit from genes that convey some drought tolerance. However, such genes are likely to exist only in stands located long distances away. Pollen dispersal in the upper layer of the atmosphere is possible, where it can be transported long distances but is also exposed to potentially damaging high UV radiation levels. Modeling approaches at the landscape level, taking into account pollen release, viability and deposition characteristics, suggest that viable oak pollen can be dispersed up to 100 km (Schueler et al., 2005).

Adaptation facilitated by genetic diversity

Local adaptation through natural selection results in the development of a phenotype that optimizes response to environmental pressures, with this phenotype corresponding to the highest fitness in the population. Under a changing environment, the required optimum is continuously shifting, but there is a time lag before this optimum phenotype is developed (by which time the environment may have changed again) (Bürger and Krall, 2004). The lag causes a reduction of fitness, with the risk that fitness will drop to a critical level too low to allow the population to replace itself (Bürger and Lynch, 1997). The lag can be compensated for in two complementary ways:

- Maintaining a large, genetically variable population with high rates of fecundity (Bürger and Lynch, 1995, 1997);
- The immigration of new genes with higher fitness via gene flow.

When applied to oaks, these predictions suggest that the lag can be reduced substantially if natural or artificial regeneration is used to renew forest stands. Indeed, the very high fecundity of trees and the large size of populations within most species will allow a considerable shift in a population's optimum from one generation to the next, allowing it to "track" environmental change.

While these conclusions are based on theoretical analysis only, they predict rapid evolution of oaks under environmental change, but they have not been supported by the results of experiments conducted over contemporary time scales. Large population sizes will maintain important genetic variation and hence increase the probability that



3/ *Quercus robur*, Hoperski Forest, Romania.

beneficial alleles favoring adaptation exist within the population. There is some indirect evidence of significant adaptive change over contemporary time scales from studies of genetic divergence in introduced exotic species in Europe, which may be relevant for the European oaks.

Northern red oak (*Q. rubra* L.) is a well-documented case. This species was introduced into Europe shortly after the French revolution and is now planted throughout the continent (Timbal et al., 1990). A large-scale provenance test was established in southwestern France, with collection data including progenies from introduced European stands and from the source populations in North America. Interestingly, the introduced populations, as a whole, exhibited a clear shift in the phenology of bud break and autumn leaf senescence from the source populations of the natural range (Daubree and Kremer, 1993). Although the genetic causes of genetic divergence are not precisely known, this example illustrates the capacity for rapid evolutionary change in oak. If the

changes in climate predicted for Europe come to be, then European oaks may have to respond in a similar manner as that illustrated for red oak.

How can we enhance adaptation to climate change?

The comparison between past and future trends suggests that migration and local adaptation will be differently affected by evolutionary processes. On the one hand, migration via seed dispersion will be limited if the climatic changes occur as rapidly as predicted. On the other hand, adaptation at local level via natural selection may be buffered considerably by significant inherent genetic variability and large population sizes. Interestingly, these data also showed that gene flow via pollen will enhance species migration and local adaptation, and will play a central role in species response to climate change. One can therefore anticipate different responses between species, depending on the nature of each species' geographic distribution. Species that have a continuous distribution are likely to benefit more from positive interactions between natural selection and gene flow than species that have a scattered distribution. It is also predicted that the evolutionary responses between populations located at the leading edge may differ from those at the rear end of distribution. Populations at the northern and eastern limit will be at the leading front of range shifts and may benefit from immigrating genes via pollen flow from southern latitudes; in contrast, adaptation may be more constrained at the rear edge, where populations are deprived of gene flow from "pre-adapted" populations.

Artificial measures could be implemented to enhance natural adaptive processes, especially in southern populations at the edge of the range. Suggested actions should be mainly directed towards modifying the genetic composition of stands during the regeneration process. New, nonlocal seeds (or seedlings) can be introduced. This “enrichment” introduces new genes, which may provide additional adaptive buffering capacity. With continuous directional shifts in climate, genotypes other than those of the contemporary populations eventually will become better suited to the new climate. As the climate changes, planting programs that involve moving appropriate genotypes between climate zones can accomplish in a single generation what would require several generations in nature. A newly regenerated stand with a mixed genetic composition is likely to have a greater potential to successfully regenerate in the future (i.e., greater fitness). The suitability of the introduced material used in sowing or planting should be determined based either on results of provenance tests or on projected future bioclimatic envelopes (if no provenance test data are available).

Guidelines on the transfer range for the direction and distance of movement of reproductive material can be developed from the geographical patterns observed in multisite provenance tests. Oak provenance tests were established since the mid 1900s, and have shown congruent geographical variation among species (Kleinschmit, 1993). The continuous or clinal patterns of variation that follow environmental gradients were observed for most traits (Ducouso et al., 1996; Deans and Harvey, 1995,1996; Liepe, 1993). This should therefore ease the choice of source populations. However, the final decision on the type of material to introduce into an area should be based on the potential impact of the new material on the overall fitness of populations rather than on the suitability of individual trait characteristics. Hence an overall meta-analysis should be carried out across all existing provenance tests in Europe to delineate seed zones for operational use.

Conclusion

This review outlines the inherent adaptive capacities of oak species to environmental changes, as witnessed by their history during natural warming over the last postglacial period. It predicts that substantial evolutionary shifts can be expected in a limited number of generations due to the high level of genetic diversity in oaks, and that gene flow will be an important driver of adaptive evolution.

To enhance their adaptive potential, it is recommended that the genetic diversity of local populations be increased by mixing local stock with seeds (or seedlings) from external sources during regeneration. Guidelines on the direction and distance of seed (or seedlings) transfers should be based on the results of up-to-date scientific evidence from studies in ecology and genetics, and on information on the patterns of geographic variation observed in existing provenance tests.

Although historical patterns have not been reconstructed in as much detail for other forest species as for oaks, some extrapolation to other species is warranted. Information from other species on the level of genetic variation, the extent of pollen flow, the existence of other inter-fertile species, and the pattern of distribution of the species (scattered or widespread) are important indicators of the potential adaptive responses of trees to climate change.

Photographers. Title page: Alexis Ducousso (*Quercus robur*). Photos 1-3: Alexis Ducousso.

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