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 hybridisation were the main processes that permitted oak 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 favourable 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 favour 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 should be increased by 'mixing' local stock with non-local 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 data from existing provenance tests.

Introduction

Concerns about the adaptation of trees to ongoing climatic changes have been repeatedly raised, particularly due to the rapid rate of environmental change relative to the long life span of trees (Aitken et al. 2008). Indeed recent climatic predictions released by the Intergovernmental Panel on Climate Change raised considerably the magnitude of the earlier estimates of temperature changes by the end of this century (Solomon et al. 2007). Trees, being long-lived organisms, exhibit lower evolutionary rates than short generation species (Smith and Donoghue 2008), so there is some concern that the pace of evolutionary change may not match environmental change. Trees, in common with other living plants, have experienced similar or larger environmental changes over longer time periods during the recurrent interglacial periods (Dynesius and Jansson 2000). Although the rates of environmental change were lower then than is now occurring in response to climate change, the evolutionary mechanisms may be similar. It is therefore of utmost importance to reconstruct the evolutionary trajectories of trees in response to previous climates, to help inform current decision making

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about climate change. Furthermore there is a growing body of evidence from different sources (Quaternary evolutionary history; observations from population and species transfers; provenance experiments) that trees may have resources and mechanisms to respond to climate change (Kremer, 2007). 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). Oak population variation has been monitored extensively from the molecular to the phenotypic level, making it possible to document the spatial and temporal differences in genetic diversity across Europe. Assembling information from phylogeography, paleobotany and provenance research, this paper shows how oaks have responded rapidly to environmental change in the past, despite their low evolutionary rate at the gene level. Furthermore, the mechanisms that trees are likely to exploit in response to ongoing climatic changes will be explored, particularly regarding migration, local adaptation or extirpation.

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

The earth's climate has been dominated during the quaternary era by the succession of more than 15 glacial and interglacial periods. Glacial periods lasted on average from 70 to 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 distributions, placing them in different habitats over time and space. These changes also represented very severe selection filters. Indeed, extinctions of European forest tree species occurred between 2.4 to 1.7 million years ago, during the early severe glacial cycles of the Quaternary period. Many species that existed in Europe at the end of the Tertiary, based on fossil evidence, disappeared and are now only present in North America and/or Asia (e.g. species belonging to the *Fagaceae* genera, such as *Lithocarpus* and *Castanopsis*). There has been no tree species extinction during the most recent periods, suggesting that extant tree species in Europe demonstrated an efficient ability to migrate and adapt to environmental change. Quaternary evolutionary history suggests, therefore, that these species have developed mechanisms to help reduce the likelihood of extinction, despite the drastic environmental changes. Recent investigations in evolutionary and population genetics allowed the identification of at least four of those mechanisms: rapid migration, extensive gene movement through pollen dispersal, interspecific hybridisation 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 (Cheddadi et al. 2005). 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 the pollen fossil remains (Brewer et al.

2002) showed that all refugial sites were 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[1] oaks increased in abundance in mountainous areas (Pyrénées, South-eastern Alps and Carpathians). 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 centre and east due to the Alps and the Carpathian mountains. The velocity of oak migration during the post glacial recolonisation period (between 15,000 to 6,000 BP) averaged 500 m year^{-1} (Brewer et al. 2002, Huntley and Birks 1983), reaching in some cases up to 1,000 m year^{-1} (Brewer et al. 2005). These figures are much larger than predicted by migration models based on dispersal agents. However, if rare long distance dispersal (LDD) events (Nathan 2006) are included in the models, then the overall expansion rate generated by the aggregation of the many populations that were founded by the LDD events may account for these rapid migration rates. Rates of occurrences of LDD events as low as 10^{-4} may be sufficient to account for the rapidity of the expansion, as deduced from fossil pollen records (Le Corre et al. 1997, Bialozyt et al. 2006). Considering the very high fecundity of oaks, LDD may have occurred repeatedly even if the frequency was low.

Extensive gene flow through pollen dispersal
As migration proceeded northwards from the different source populations, the colonisation routes merged in central Europe resulting in genetic homogenisation as these different populations interbreed. The resulting genetic diversity was so great that the genetic imprint of the original refugia from which they were derived was virtually erased. Large scale analysis of nuclear gene diversity across Europe has consistently found very low levels of genetic differentiation among modern oak populations, regardless of the markers used (Zanetto and Kremer 1995, Mariette et al. 2002), which may be attributed to extensive gene flow. Pollen flow dynamics in Quercus petraea or Q. robur 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, and pollen dispersion curves are characterised 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 colonising populations.

Hybridisation as a colonisation process
A very intriguing result of the pan-European genetic survey of chloroplast DNA diversity was the almost complete sharing of chloroplast genomes between different

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[1] Before present.

oak species when they occupy the same forest stand (Petit et al. 2002). For example, when *Q. petraea* and *Q. robur* are present in the same forest they usually share the same chloroplast genetic variant; they may share a different chloroplast variant in a different forest where they coexist just a few km away. The almost complete sharing of chloroplast variants among the two species occupying the same stand was observed across the natural distribution of the oaks, suggesting that hybridisation was common and widespread during post glacial colonisation. Because chloroplast genomes are of maternal origin, hybrids will inherit the chloroplast of the female parent. Hybridisation may play an important role in the colonisation process, since repeated hybridisation events accelerate species migration and succession rates. The effect of hybridisation can be traced, as described in detail by Petit et al. (2003) for *Q. petraea* and *Q. robur*. Because *Q. robur* tends to be a more pioneering species than *Q. petraea*, it was assumed that *Q. robur* was present at the northern edge of the oak migration front, and that *Q. petraea* was somewhat behind it, but still capable of hybridising with *Q. robur* through pollen flow. If the first generation hybridisation is followed by later backcrosses (e.g. between hybrids and parents) with *Q. petraea* as male parent, then successive introgression will lead to restoration of *Q. petraea* trees within the *Q. robur* stand, consequently enhancing species succession. The peculiar role of hybridisation shows that colonisation of newly available territories by oaks (for instance following successive ice ages) is facilitated by interspecific gene exchanges, allowing one species to rapidly invade new sites despite colonisation by the other species.

Rapid adaptation

After colonising a new site, the newly established populations begin to differentiate genetically from the source populations from which they were derived. For obvious biological reasons, it is impossible to monitor evolutionary change of a given population from one generation to the next, but some indirect assessment of evolutionary change from today's genetic divergence among populations planted in provenance tests is possible. There is now evidence that the genetic divergence among extant populations resulted from adaptive evolution due to local selection from the time of establishment of populations on new sites (Kremer et al. 2010). Assuming that the Spanish and Italian-Balkan refugial populations were genetically separated for more than 100,000 years during the last glacial period, genetic differentiation may have accumulated between the two source populations and may be partly responsible for the differentiation between extant populations of different refugial origin. In two previous papers (Kremer et al. 2002, Kremer et al. 2010), it was shown that there was little evidence of genetic separation relating to the original source population, based upon the patterns of variation observed in current provenance tests. Indeed most phenotypic traits show clinal variation, with different clinal patterns of variation for different traits (Ducousso 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 usually 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. However, there is little information on the precise rate of evolution during adaptation. Theoretical approaches have however, shown that the interaction of extensive gene flow and strong diversifying selection will accelerate differentiation of complex multi-locus traits (Le Corre and Kremer 2003) and achieve adaptation in less than 20 generations. The rapid process is generated by allelic associations among different loci that increase population differentiation of adaptive traits in response to diversifying selection. The mechanism is enhanced by gene flow that provides the diversity needed to create different allelic associations. The overall process is accelerated if the number of loci contributing to the trait of interest increases.

How will evolutionary processes stimulate adaptive responses under climate change?

The response of natural tree populations to climate changes has been sketched 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 among the different evolutionary processes just described. It is important to evaluate how natural mechanisms will be activated to determine if human interception would be needed. Predictions on the potential impact of climate change on oak populations are made in the following sections, based on historical as well as on contemporary records.

Migration by seed constrained by natural seed dispersion

There has been considerable research on the shift of bioclimatic envelopes (i.e. the geographic range over which environmental conditions are favourable for the growth of a particular species) of trees species induced by global change. This approach involves constructing a statistical relationship between the current geographic distribution of a given species and the climatic data for the distribution range. This relationship can then be projected under the different IPCC gas emission and climatic scenarios, to predict where the same envelope might be located in the future (Thuiller et al. 2005, 2006). It is beyond the scope of this paper to discuss the limitations of the approach (Hampe 2004), but predicted future bioclimatic envelopes provide some rough indications on the distance that populations would need to be shifted to remain under the "same" bioclimatic conditions. In the case of *Q. petraea*, a shift of 200 to 500 km North and North East by the end of the current century is predicted, depending on the level of greenhouse gas emissions (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 post glacial recolonisation period and these data can be used to assess the likelihood that the oak will be able to migrate quickly enough in response to the displacement of the envelope. Palinological records indicate migration velocities

ranging from 500 to 1,000 m year^{-1}, amounting to a displacement of 50 to 100 km in one century. At maximum, 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. However, it is clear that dispersion by natural means will not allow the species to track rapidly enough the displacement of the bioclimatic envelope.

Hybridization facilitating migration and succession
While there are only two temperate oaks species (*Q. petraea* and *Q. robur*) in Europe, there are more than 20 species and sub species located in central and Mediterranean areas (Schwarz 1964). They belong to two main oak sections (*cerris* and *lepidobalabnus sensus* Camus) and hybridisation within sections is quite common (Curtu et al. 2007, Lepais et al. 2009). Climatic change is expected to cause species migrations, with more range overlaps and competition for new niches on the newly invaded sites. Consequently, this might be expected to increase the opportunities for hybridisation and introgression among species. There are two ways in which hybridisation may enhance adaptation of oak populations to climate change:

- By accelerating species migration, just as hybridisation permitted *Q. petraea* to migrate northwards during the postglacial period, by repeated unidirectional interspecific crosses with *Q. robur*. Similar hybridisation events may occur with other species combinations involving Mediterranean oaks, facilitating the establishment of Mediterranean species at more northerly latitudes. Hence hybridisation may help overcome the limitations of species migration via seed that was limited to less then 100 km because pollen is dispersed over longer distances than seed.
- Hybridisation may facilitate establishment and species succession on new sites. Oak species are characterised 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 hybridisation will accelerate the migration of species, it will subsequently facilitate their establishment on the most suitable sites, those that are already occupied by temperate species. In the long run, this process will end in the replacement of one species by another, which may accelerate ecological succession.

Finally, the combination of introgression and selection may further contribute to novel allelic combinations, enhancing the adaptation of newly introgressed forms (Seehauzen 2004). The outcome is largely dependent on the relative fitness of introgressed forms versus those of the parental species under the new environmental conditions, but these suggestions are speculative at this time. The process may be extremely rapid if transgressive segregation occurs, but could require several

successive generations, including some backcrosses, to increase the fitness of the introgressed forms.

Gene flow enhancing adaptation
Local adaptation can be increased by "incoming genes" via pollen from populations 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. 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. Subsequent changes might be unfavourable or favourable, depending on the source population (Lenormand 2002). 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 to receive 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. Extensive research has been done on gene flow in forest trees at a rather narrow spatial scale (Austerlitz et al. 2004, Smouse and Sork 2004). Most of these theoretical and experimental studies have shown that gene dispersion has both local and long-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. Modelling approaches at the landscape level, taking into account pollen release, viability and deposition characteristics suggest that viable pollen of oak can be dispersed up to 100 km (Schueler et al. 2005; Schueler and Schlunzen 2006). Pollen dispersal distances are usually estimated based on observations recorded over a single generation (Austerlitz et al. 2004) but estimates of dispersal distances over a few successive generations is lacking.

Adaptation facilitated by genetic diversity
Local adaptation is the process by which natural selection results in the development of a phenotype that optimises the response to the 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 this fitness level reaches a critical level that is too low to allow the population replace itself (Bürger and Lynch 1997). The lag can be maintained at a tolerable level 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. However, there is experimental evidence from model plant species (having shorter generation cycles than oak), that rapid adaptive evolution is possible in situations where population sizes are large (Bell and Gonzalez 2009, Stockwell et al. 2003). Large population sizes will maintain important genetic variation, and hence increase the probability that beneficial alleles favouring 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. 1994). A large-scale provenance test was established in south-western France, and the collection included progenies derived from introduced European stands and from the source populations in North America. Interestingly, the introduced and now naturalised populations, as a whole, exhibited a clear shift in the phenology of bud break and autumn leaf senescence compared with provenances introduced directly from the natural range (Daubree and Kremer 1993). Although the genetic causes of the 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 are realised, then European oaks may have to respond in a similar manner to that illustrated for red oak.

How can we enhance adaptation to climate change?
A comparison of past with projected future trends suggest that migration and local adaptation will be differently affected by evolutionary processes. On one hand, migration via seed dispersal 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 show that gene flow via pollen will enhance species migration and local adaptation, and will play a central role in species responses 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 a 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 "preadapted" populations.

Artificial measures could be implemented to enhance natural adaptive processes, especially in southern populations at the edge of the range. Suggested actions should mainly be directed towards modifying the genetic composition of stands during the regeneration process. New, non local 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 programmes 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 multi-site 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 (Ducousso 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.

Conclusions

This review outlines the inherent adaptive capacities of oak species to environmental changes, as witnessed by their history during natural warming over the last post glacial period. It predicts that substantial evolutionary shifts can be expected in a limited number of generations due to their high level of genetic diversity, 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 could 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 the 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 interfertile 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.

References

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. and Curtis-McLane, S. 2008. Adaptation, migration, or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1: 95-111.

Austerlitz, F., Dick, C.W., Dutech, C., Klein, E., Oddou-Muratorio, S., Smouse, P.E. and Sork, V.L. 2004. Using genetic markers to estimate the pollen dispersal curve. *Molecular Ecology* 13: 937–954.

Bell, G. and Gonzalez, A. 2009. Evolutionary rescue can prevent extinction following environmental change. *Ecology Letters* 12: 942-948.

Bialozyt, R., Ziegenhagen, B. and Petit, R.J. 2006. Contrasting effects of long distance seed dispersal on genetic diversity during range expansion. *Journal of Evolutionary Biology* 19: 12-20.

Brewer, S., Cheddadi, R., De Beaulieu, J.L. and Reille, M. 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. *Forest Ecology and Management* 156: 27-48.

Brewer, S., Hely-Alleaume, C., Cheddadi, R., De Beaulieu, J., Laurent, J. M. and Cuziat, J. 2005. Postglacial history of Atlantic oakwoods: context, dynamics and controlling factors. *Botanical Journal of Scotland* 57: 41-57.

Bürger, R. and Krall, C. 2004. Quantitative-genetic models and changing environments. In *Evolutionary Conservation Biology*. Eds. Ferrière, R., Dieckmann, U. and Couvet, D., Cambridge University Press, pp. 171–187.

Bürger, R. and Lynch, M. 1995. Evolution and extinction in a changing environment: a quantitative-genetic analysis. *Evolution* 49: 151-163.

Bürger, R. and Lynch, M. 1997. Evolution and extinction in changing environments. In *Environmental Stress, Adaptation, and Evolution*. Eds. Bijlsma, R. and Loeschke, V., Birkhäuser Verlag, pp. 209-239.

Cheddadi, R., De Beaulieu, J.L., Jouzel, J., Andrieu-Ponel, V., Laurent, J.M., Reille, M., Raynaud, D. and Bar-Hen, A. 2005. Similarity of vegetation dynamics during interglacial periods. *Proceedings National Academy Sciences USA* 39: 13939-13943.

Curtu, A.L., Gailing, O. and Finkeldey, R. 2007. Evidence for hybridisation and introgression within a species-rich oak (*Quercus spp*.) community. BMC *Evolutionary Biology* 7: 218.

Daubree, J.B. and Kremer, A. 1993. Genetic and phenological differentiation between introduced and natural populations of *Quercus rubra* L. *Annals of Forest Science* 50 (Suppl. 1): 271–280.

Deans, J.D. and Harvey, F.J. 1995. Phenologies of sixteen European provenances of sessile oak growing in Scotland. *Forestry* 68: 265-273.

Deans, J.D. and Harvey, F.J. 1996. Frost hardiness of 16 European provenances of sessile oak growing in Scotland. *Forestry* 69: 5-11.

Ducousso, A., Guyon, J.P. and Kremer, A. 1996. Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (*Quercus petraea* (Matt.) Liebl.). *Annals of Forest Science* 53: 775-782.

Ducousso, A., Louvet, J.M., Jarret, P. and Kremer, A. 2005. Geographic variations of sessile oaks in French provenance tests. In *Proceedings of the Joint Meeting of IUFRO Working Groups Genetic of Oaks and Improvement and Silviculture of Oaks*. Eds. Rogers, R., Ducousso, A. and Kanazashi, A., FFPRI (Forestry and Forest Products Research Institute), Scientific Meeting Report 3, Tsukuba, Japan, pp 128-138.

Dynesius, M. and Jansson, R. 2000. Evolutionary consequences of changes in species geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences of the United States of America* 97: 9115–9120.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography* 13: 469–476.

Hays, J.D., Imbrie, J. and Shackleton, N.J. 1976. Variations in the Earth's orbit: pacemaker of the ice ages. *Science* 194: 1121–1132.

Huntley, B. and Birks, H.J.B. 1983. *An Atlas of Past and Present Pollen Maps for Europe: 0–13000 Years Ago*. Cambridge University Press, London, 667 pp.

Kleinschmit, J. 1993. Intraspecific variation of growth and adaptive traits in European oak species. *Annals of Forest Science* 50: 166s-186s.

Kremer, A. (Ed.) 2002. Range wide distribution of chloroplast DNA diversity and pollen deposits in European white oaks: inferences about colonisation routes and management of oak genetic resources. *Forest Ecology and Management* 156: 1-223.

Kremer, A. 2007. How well can existing forests withstand climate change? In *Climate change and forest genetic diversity: Implications for sustainable forest management in Europe*. Eds. Koskela, J., Buck, A. and Tessier du Cros, E., Bioversity International, Rome, Italy, pp. 3-17.

Kremer, A., Kleinschmit, J., Cottrell, J., Cundall, E.P., Deans, J.D., Ducousso, A., Konig, A.O., Lowe, A.J., Munro, R.C., Petit, R.J. and Stephan, B.R. 2002. Is there a correlation between chloroplastic and nuclear divergence, or what are the roles of history and selection on genetic diversity in European oaks? *Forest Ecology and Management* 156: 75-87.

Kremer, A., Le Corre, V., Petit, R.J. and Ducousso, A. 2010. Historical and contemporary dynamics of adaptive differentiation in European oaks. In *Molecular Approaches in Natural Resource Conservation*. Eds. DeWoody, A., Bickham, J., Michler, C., Nichols, K., Rhodes, G. and Woeste, K., Cambridge University Press, pp. 101-122.

Le Corre, V., and Kremer, A. 2003. Genetic variability at neutral markers, quantitative trait loci and trait in a subdivided population under selection. *Genetics* 164: 2005-2019.

Le Corre, V., Machon, N., Petit, R.J. and Kremer, A. 1997. Colonisation with long-distance seed dispersal and genetic structure of maternally inherited genes in forest trees: a simulation study. *Genetical Research* 69: 117-125.

Lenormand, T. 2002. Gene flow and the limits to natural selection. *Trends in Ecology and Evolution* 17: 183–189.

Lepais, O., Petit, R.J., Guichoux, E., Lavabre, E., Alberto, F., Kremer, A. and Gerber, S. 2009. Species relative abundance and direction of introgression in oaks. *Molecular Ecology* 18: 2228-2242.

Liepe, K. 1993. Growth chamber trial on frost hardiness and field trial on bud burst of sessile oak (*Quercus petraea* Liebl. and *Q. robur* L.). *Annals of Forest Science* 50: 208-214.

Mariette, S., Cottrell, J., Csaikl, U.M., Goikoechea, P. Konig, A., Lowe, A.J, Van Dam, B.C., Barreneche, T., Bodénès, C., Streiff, R., Burg, K., Groppe, K., Munro, R.C., Tabbener, H. and Kremer, A. 2002. Comparison of levels of genetic diversity detected with AFLP and microsatellite markers within and among mixed *Q. petraea* (Matt.) Liebl. and *Q. robur* L. stands. *Silvae Genetica* 51: 72-79.

Nathan, R. 2006. Long distance dispersal in plants. *Science* 313: 786-788.

Petit, R.J., Bodénès, C., Ducousso, A., Roussel, G. and Kremer, A. 2003. Hybridization as a mechanism of invasion in oaks. *New Phytologist* 161: 151-164.

Petit, R.J., Csaikl, U.M., Bordacs, S., Burg, K., Coart, E., Cottrell, J., Van Dam, B.C., Deans, J.D., Dumolin-Lapegue, S., Fineschi, S., Finkeldey, R., Gillies, A.C.M., Glaz, I., Goiecoechea, P.G., Jensen, J.J., König, A.O, Lowe, A.J., Madsen, S.F., Matyas, G., Munro, R.C., Olalde, M., Pémonge, M.H., Popescu, F., Slade, D., Tabbener, H., Taurchini, D., De Vries, S.M.G., Ziegenhagen, B. and Kremer, A. 2002. Chloroplast DNA variation in European white oaks: Phylogeography and patterns of diversity based on data from over 2,600 populations. *Forest Ecology and Management* 156: 5-26.

Schueler, S. and Schlünzen, K.H. 2006. Modelling of oak pollen dispersal on the landscape level with a mesoscale atmospheric model. *Environ Model Assess* 11: 179-194.

Schueler, S., Schlünzen, K.H. and Scholz, F. 2005. Viability and sensitivity of oak pollen and its implications for pollen-mediated gene flow. *Trends in Ecology and Evolution* 19: 154-161.

Schwarz, O. 1964. *Quercus* L. In *Flora Europaea*. Vol. 1: Lycopodiaceae to Platanaceae. Eds. Tutin, T. G., Heywood, V. H., Burges, N. A., Valentine, D. H., Walters, S. M. and Webb, D. A., Cambridge University Press, Cambridge, pp. 61-64.

Seehauzen, O. 2004. Hybridization and adaptive radiation. *Trends in Ecology and Evolution* 19: 198-207.

Smith, S.A. and Donoghue, M.J. 2008. Rates of molecular evolution are linked to life history in flowering plants. *Science* 322: 86-89.

Smouse, P.E. and Sork, V.L. 2004. Measuring pollen flow in forest trees: an exposition of alternative approaches. *Forest Ecology and Management* 197: 21–38.

Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L. (Eds.) 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, USA.

Stockwell, C.A., Hendry, A.P. and Kinnison, M.T. 2003. Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution* 18: 94-101.

Streiff, R., Ducousso, A., Lexer, C., Steinkellner, H., Gloessl, J. and Kremer, A. 1999. Pollen dispersal inferred from paternity analysis in a mixed oak stand of *Quercus robur* L. and *Q. petraea* (Matt.) Liebl. *Molecular Ecology* 8: 831-841.

Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T. and Prentice, J.C. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* 102: 8245–8250.

Thuiller, W., Lavorel, S., Sykes, M.T. and Araújo, M.B. 2006. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe? *Diversity and Distributions* 12: 49–60.

Timbal, J., Kremer, A., Le Goff, N. and Nepveu, G. (Eds.) 1994. *Le chêne rouge d'Amérique*. Editions de l'INRA, Paris, France, 564p.

Valbuena-Carabana, M., Gonzalez-Martinez, S.C., Sork, V.L., Collada, C., Soto, A., Goicoechea, P.G. and Gil, L. 2005. Gene flow and hybridisation in a mixed oak forest (*Quercus pyrenaica* Willd. and *Quercus petraea* (Matt.) Liebl.) in central Spain. *Heredity* 95: 457-485.

Zanetto, A. and Kremer, A. 1995. Geographical structure of gene diversity in *Quercus petraea* (Matt.) Liebl. I. Monolocus patterns of variation. *Heredity* 75: 506-517.