

Strategies for conserving forest genetic resources in the face of climate change

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Abstract: Conservation of genetic diversity is important for continued evolution of populations to new environments, as well as continued availability of traits of interest in genetic improvement programs. Rapidly changing climates present new threats to the conservation of forest genetic resources. We can no longer assume that in situ reserves will continue to preserve existing genetic diversity. Management of reserves should become more active. In some reserves, existing genetic diversity should be preserved by creating stands that are more resistant to threats using silvicultural treatments such as thinning and prescribed burning. In other reserves, natural selection and adaptation to changed environments should be promoted by increasing within population genetic diversity and promoting gene flow. This may be done by locating reserves in areas of high environmental heterogeneity, minimizing fragmentation, and using assisted colonization to increase genetic diversity by establishing populations adapted to future climates within or adjacent to reserves. Threats to native stands from climate change and other interacting threats should bring a renewed importance to ex situ collections, particularly for rare and disjunct populations and those at the warmer and drier edges of a species range. Assisted colonization to move threatened populations to new environments must be considered as an additional conservation measure.

Key words: Climate change, genetic conservation, adaptation

Introduction

Conserving genetic diversity is an essential component of sustainable forest management. The ability of trees and other forest plants to evolve to resist pests and adapt to changing climates depends upon genetic diversity within species. Genetic diversity is also critical for artificial selection and breeding for forest products and other environmental services. We have an ethical obligation to protect genetic diversity for future generations, partly because we cannot predict which traits will be important in

the future. The urgency for gene conservation has become greater with increasing evidence of global climate change and associated risks of extirpation of species and populations. The Intergovernmental Panel on Climate Change (IPCC) projects that global average surface temperatures will rise about 1.8 to 4.0 °C during the 21st century, and up to 30% of the world's species will be at increased risk of extinction (Intergovernmental Panel on Climate Change, 2007).

Although much of the focus of national programs of gene conservation has been on agricultural

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species, increased threats to native wild species from climate change bring increased attention to forest trees. Forest trees define the essential characteristics of forests, and their long generation intervals put them at particular risk for maladaptation to climate change (St.Clair & Howe, 2007). In this paper, we review threats to genetic diversity of forest plants, discuss factors that can be used to prioritize species and populations for conservation, and discuss strategies for gene conservation. Although other reviews of forest gene conservation exist, we focus specifically on gene conservation threats, priorities, and strategies in relation to climate change.

Threats to genetic diversity

Threats to forest genetic diversity include threats to species, populations, and genetic variation within populations. These threats are both natural and human-caused, although distinguishing which are which is increasingly difficult. Habitat loss and deforestation from urbanization, conversion to agriculture, overgrazing, overharvesting without regeneration, and replacement of native forests with non-native plantations are pervasive threats to forest genetic resources worldwide. The net decrease in global forest area between 2000 and 2005 was estimated to be 7.3 million hectares (FAO, 2006). These problems tend to be greatest in areas of high population pressures and poverty. Low-elevation forests tend to be the most threatened, and this is significant because adaptive genetic variation tends to be geographically structured. Habitat loss and deforestation can lead to fragmentation of remaining native stands, which can contribute to the decline of those stands by disrupting natural patterns of migration (gene flow) and reducing effective population sizes.

Even where forests are regenerated, management practices can negatively impact genetic resources if straight, fast-growing, more pest-resistant trees are selectively harvested, and poor trees are left as seed trees (dysgenic selection). Replacement of native stands with very different species or genetically distinct populations can lead to the loss of genetic diversity. For example, the wide use of grass and forb cultivars in restoration can lead to the loss of significant genetic variation in native populations of these species. Poor management can contribute

to losses from fire, pathogens, insects, and invasive species.

Climate change alone represents a considerable threat to genetic diversity (discussed below); but climate change may also exacerbate threats from natural disturbances such as disease, insects, fire, and extreme weather. Fires are expected to be more frequent and increasingly severe with increasing temperatures and corresponding droughts (Westerling et al., 2006). Native insects and diseases may become epidemic as a result of climate change (Woods et al., 2005; Carroll et al., 2006). Climatic extremes may become more frequent in the future, contributing to losses of forest genetic resources from drought, wind, and even, paradoxically, extremes in late spring and early fall frosts. Threats to genetic diversity from climate change and natural disturbances are further complicated by interactions with habitat loss, deforestation, and poor management.

Vulnerability and prioritization of species and populations for gene conservation

Climate change will have widespread and long-term consequences for many species. It has become increasingly clear that triage may be necessary to prioritize species and populations for conservation. The simple answer for prioritization is to give greater priority to those species and populations at greatest risk. Determining those species and populations at greatest risk, however, is not an easy task. Risk is defined as the product of the impact of an occurrence (i.e. the loss of genetic diversity) and the probability of that occurrence. Some level of uncertainty will be associated with estimating impact and probability, and so that must also be considered.

Impact depends on the value of the species, population, and genetic variants that are at risk of being lost, including value to society and to the ecological integrity of ecosystems. Thus, we might place greater priority on economically important species. An example is *Pseudotsuga menziesii* (Mirb.) Franco, a keystone species that defines the components and processes inherent in many ecosystems in western North America. We might place greater priority on populations with unique and valuable genetic variants. Populations of *Pinus radiata* D.Don on Guadalupe Island, Mexico, or

populations of *Picea glauca* (Moench) Voss in the Ottawa Valley, Canada, are examples of populations that deserve a high priority because of their unique genetic characteristics that may be valuable to future generations (disease resistance in Guadalupe Island *Pinus radiata* and fast growth in Ottawa Valley *Picea glauca*; Ledig et al., 1998). Despite the intuitiveness of placing a high priority on economically important species, these are also the species that may be well conserved in breeding programs (Lipow et al., 2002, Lipow et al., 2003). Society also values that which is rare, and so threatened species or populations, or species that are widespread but rare throughout much of their range, may be given higher priority. Such is the case for *Pinus torreyana* Parry ex Carrière in California, USA (Ledig et al., 1998) and Mexican spruces (Ledig et al., 2000).

The probability that genetic diversity will be lost depends on human factors, natural processes, and their interactions. In evaluating human factors, we must consider the probability of deforestation, land-use change, or management practices at specific locations. Locality is important because genetic diversity is spatially patterned, and impact depends on which genetic diversity is lost. Predicting those probabilities is difficult because of uncertain political and economic changes. Predicting the effects of specific management practices, such as dysgenic selection or replacement of local native populations with populations from other localities, depends on knowledge of genetic structure and pattern, something that may not be well known.

The probability of loss from natural processes depends on the vulnerability of a species or population to changing biotic or abiotic environments (Table 1). In the long-run, plant populations may avoid extirpation and adjust to rapidly changing environments by evolving new adaptations through natural selection, or migrating to new habitats (Davis & Shaw, 2001; Davis et al., 2005; Savolainen et al., 2007; Aitken et al., 2008). In the shorter term, acclimating (i.e. relying on phenotypic plasticity, defined as the capacity of individual plants to change phenotypes in response to changes in the environment) may be important for maintaining existing populations until evolutionary adaptation occurs. Species or populations that are more vulnerable to environmental change are those

Table 1. Species and populations most vulnerable to climate change.

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- Rare species
 - Species with long generation intervals (e.g., long-lived species)
 - Genetic specialists (species that are locally adapted)
 - Species with limited phenotypic plasticity
 - Species or populations with low genetic variation
 - Small populations
 - Species influenced by past genetic bottlenecks
 - Inbreeding species
 - Species or populations with low dispersal and colonization potential
 - Fragmented, disjunct populations
 - Populations at the trailing edge of climate change
 - Populations with “nowhere to go”
 - Populations threatened by habitat loss, fire, disease, or insects
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with low phenotypic plasticity, low genetic variation (particularly as expressed in adaptive traits), and low potential for migration to new habitats via pollen, seeds, or vegetative propagules, all characteristics of rare and endemic species. Furthermore, species with low potential for generation turnover (e.g., trees) are particularly vulnerable as climates continue to change without the possibility of natural selection or migration, which requires generation turnover.

Low genetic variation can result from genetic drift within small populations and species differences in mating systems. In the case of highly selfing species, the impact of inbreeding and low genetic variation on population fitness is less, and genetic variation among populations is more important, particularly when considering sampling strategies for gene conservation. Although genetic variation in adaptive traits (i.e. those traits that influence survival and reproduction) is particularly important, we may also seek to maintain genetic variation in other economically important traits such as wood properties. Because most traits of interest are quantitatively inherited, this must be considered when designing gene conservation strategies.

Gene flow among populations, through pollen, seed, or vegetative propagules, is an important process for incorporating new genetic variation into a population. The importance of gene flow depends on the nature of the new genetic variation (which depends on the geographic structure of genetic variation) and the amount of gene flow. Gene flow from adjacent populations that are not genetically different in adaptive traits will not be useful for adapting to climate change. Highly heterogeneous environments such as mountainous areas are probably good targets for conservation because they are likely to have greater variation in adaptive traits, and shorter distances between genetically distinct populations. However, differences in flowering phenology may inhibit gene flow in these same areas. Fragmentation becomes an important factor because greater fragmentation decreases the potential for gene flow among populations. Inherent in evaluating the role of gene flow and fragmentation in prioritizing conservation areas is an understanding of levels and distances of gene flow and the structure of genetic variation across the landscape. In landscapes with plantations interspersed among native populations, it would be helpful to know the genetic composition of the plantations, particularly with respect to adaptive genetic variation.

Species with a high potential for migration may be less vulnerable than species with low migration potential. Populations at species margins deserve higher priorities for conservation because they may have unique genetic characteristics resulting from adaptation to unique environments at the edges of the species realized niche. Furthermore, populations at species margins are likely to be under greater stress from maladaptation and interspecific competition, leading to lower fecundity and lower population densities (Case & Taper, 2000), and may receive considerable gene flow from central populations, further inhibiting local adaptation and reducing mean fitness (Garcia-Ramos & Kirkpatrick, 1997). In a warming climate, however, gene flow may promote migration at the leading edge (i.e. higher latitudes or higher elevations) by introducing variation from populations that inhabit warmer climates. Conversely, populations at the trailing edge may have a higher probability of extirpation and may, thus, deserve a higher priority for conservation (Hampe

& Petit, 2005). Of greatest concern are populations with nowhere to go, such as populations at the tops of mountains.

Generation interval is another important consideration in assessing response to climate change. The long generation intervals of forest trees are expected to inhibit adaptation to future climates. In contrast, short-lived annuals and perennials may adapt easier because of frequent generation turnover and episodes of natural selection (Lenoir et al., 2008). Nonetheless, forest trees have a higher probability of persistence once they become established because of their longevity and phenotypic plasticity. Without opportunities for selection and reproduction, tree populations will become increasingly maladapted. St.Clair and Howe (2007) found that naturally-regenerated stands of *Pseudotsuga menziesii*, or stands planted with local seed sources, will have a high risk of maladaptation by the end of the century, a period of time that is well within the lifetime of many stands. Populations expected to be adapted to future climates are located 500 to 1000 m lower in elevation and 2 to 5 degrees latitude further south. In simulation studies, slow generation turnover was largely responsible for the inability of *Pinus sylvestris* L. populations to track their adaptive optimum with changing climates (Savolainen et al., 2004). The number of generations required for populations to evolve to new optima for future climates may be considerable; as many as 12 generations for *Pinus contorta* Douglas ex Loudon populations in southern British Columbia and *Pinus sylvestris* populations in Eurasia (Rehfeldt et al., 2001; Rehfeldt et al., 2002). Nonetheless, long generation times and persistent populations may be advantageous for gene conservation. Although the potential for adaptation to new climates is reduced, these persistent populations will continue to act as stores of in situ genetic variation, and should be able to contribute genetic diversity to adjacent populations.

If genetic variants are represented in multiple populations, the highest priority for in situ conservation should be given to populations that are more likely to persist and maintain genetic variation. On the other hand, high priority might be given to populations with unique genetic variation of high value not found elsewhere despite low genetic diversity and small population size.

Strategies to conserve genetic diversity

Two methods can be used to conserve genetic diversity: ex situ and in situ gene conservation (Table 2). Ex situ conservation refers to the collection and storage of germplasm at a site removed from its place of origin. Most often, this involves collections of seed or pollen kept in cold storage, but may also include plants grown in genetic tests, breeding orchards, and field conservation plantings. Arboreta and botanical gardens are also ex situ collections, but generally have too few individuals to be useful for conserving genetic variation. Tissue culture and DNA in genomic libraries are generally not useful for genetic conservation for restoration purposes because of current technological limitations. Ex situ gene conservation is the method predominately used in agriculture.

In situ conservation refers to conservation of genetic diversity in populations growing in their place of origin. One goal of in situ conservation is to allow normal evolutionary processes to occur (Heywood, 2008). Although often designated for reasons other than gene conservation, strict nature reserves and other types of protected areas have been viewed as important areas of in situ gene conservation. In situ conservation may also occur on non-protected lands, including those that are actively managed, particularly if normal evolutionary

processes are promoted via natural regeneration. Planting, thinning, and harvesting may be done in in situ reserves if they approximate the effects of natural processes, particularly with respect to adaptive genetic variation. Areas designated and managed specifically to promote long-term gene conservation have been called gene resource management units (Ledig, 1988; Millar & Libby, 1991).

Gene conservation becomes more complicated with rapidly changing climates. Before climate change became important, in situ reserves were thought to be places to conserve and maintain existing genetic variation. With rapidly changing climates, however, existing genetic variation will be highly vulnerable to loss. Climate change will likely lead to increased stress from drought, and warm winters may not fulfill chilling requirements for vegetative and reproductive budburst. Whole populations may be at increased threat of loss from fire, disease, and insects. Changed dynamics of interspecific competition may lead to the loss of some species. Even if populations have the capacity to adapt to changed environments, genetic variants may be lost because of strong natural selection or genetic drift. Consequently, gene conservation in in situ reserves becomes a balancing act of promoting adaptation to new climates with the potential loss of genetic variants versus maintaining existing genetic variation within each reserve.

Table 2. Strategies for gene conservation in the face of rapidly changing climates.

In situ gene conservation

- Locate reserves in areas of high environmental heterogeneity to maximize genetic diversity and gene flow within and among reserves.
- Design a network of reserves and the forest “matrix” between reserves to minimize fragmentation, maximize gene flow between conserved populations, and avoid small effective population sizes.
- Actively manage reserves to increase resistance of stands to increased stress and threats from natural disturbances such as fire, drought, disease, and insects (by thinning, prescribed fire, etc.)
- Supplement existing genetic variation by planting seedlings from populations adapted to new climates within or adjacent to reserves.

Ex situ conservation

- Give priority to collections from areas particularly threatened from fire, disease, or insects; small and disjunct populations; marginal populations at the trailing edge of climate change; and high elevation populations with “nowhere to go”.

Assisted colonization

- Move high priority populations to new locations where they are adapted to future climates.
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The maintenance of existing genetic diversity within in situ reserves may be promoted by locating reserves in areas of high environmental heterogeneity and high genetic diversity, such as might be found in mountainous areas with sharp elevational gradients. Campbell (1979) found considerable genetic variation in adaptive traits in *Pseudotsuga menziesii* within a small watershed with a 1000 m range in elevation in central Oregon. Locating reserves in areas of high diversity will also promote adaptation by allowing for high gene flow between parents adapted to different micro-environments as a result of high selection pressures. Maintaining existing genetic diversity in in situ reserves may also be promoted using silvicultural practices that make stands more resistant to natural disturbances. For example, thinning, fuels reduction, prescribed fire, and insect traps can be used to improve resistance to drought, fire, and pests. Active management of protected areas may ultimately become required to maintain ecosystem function.

Ex situ collections are an important back-up for populations that are vulnerable to fire and pests. Unique and disjunct populations at greatest risk from human or natural disturbances should be given the highest priority. Disjunct populations with small population sizes may harbor unique genetic variants due to genetic drift or selection to unique environments. Marginal populations at the warmer and drier ends of the species ranges should also be given high priority.

Establishment of species and populations at new locations where they are better adapted to future environments may be important for conserving genetic diversity. Moving species and populations to match future habitats has been called assisted colonization or assisted migration (McLachlan et al., 2007). Assisted colonization for gene conservation is a strategy that combines in situ and ex situ methods. Populations are removed from their place of origin as in ex situ conservation, but natural selection is then allowed to occur in their new habitats as in in situ conservation. Assisted colonization may be used to supplement genetic variation in existing in situ reserves to promote adaptation, either by planting within the reserves or in adjacent areas. Assisted colonization requires an understanding of the climates to which a population is adapted to, and

patterns of future climate change (St.Clair et al., 2005; Wang et al., 2006; St.Clair & Howe, 2007).

Conclusions

Genetic conservation programs must take into account the specter of climate change. Climate change may influence species priorities, sampling strategies, locations and management of in situ reserves, the role of ex situ collections, and the role of new plantations. The following recommendations should be considered when evaluating strategies for gene conservation in the face of climate change:

- Rare and endemic species should be given a high priority for genetic conservation, but present special challenges because of small population sizes, lack of biological knowledge, and policy issues that might preclude desirable management practices.
- Trees should be given a high priority for genetic conservation because of their long generation intervals and key ecosystem functions.
- Trade-offs must be evaluated between maintaining existing genetic diversity in in situ reserves and promoting natural selection and adaptation to new environments.
- Active management of in situ reserves (e.g., thinning or prescribed fire) should be used as needed to increase the resistance of stands to increased stress and threats from natural disturbances such as fire, drought, disease, and insects.
- In situ reserves should be located in areas of high environmental heterogeneity as well as in areas where unique populations occur.
- Fragmentation should be minimized to maximize gene flow between conserved populations and avoid small effective population sizes.
- As populations in in situ reserves become increasingly maladapted, seedlings from populations adapted to the new climates may be planted within or adjacent to stands to increase genetic diversity and the adaptive potential of reserves.

- Ex situ collections will become increasingly important as in situ reserve populations become threatened by climate change.
- Assisted colonization should be used to move high priority populations to new locations where they are adapted to future climates.
- Designing effective gene conservation strategies requires knowledge of the genetic structure and patterns of gene flow for species of interest.

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