

## Chapter 3.1—Genetics of Forest Trees

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### Summary

Combining data from provenance test studies with our current understanding of predicted climate change can be a powerful tool for informing reforestation efforts. However, the limitations of both sources of data need to be understood to develop an approach to ecological restoration that reduces risk and promotes the highest chance of successful reforestation.

### Introduction

Climate change is anticipated to cause dramatic shifts in climate across the Sierra Nevada, including increased frequency and severity of wildfires (Safford et al. 2012). Reforestation may be an important component of ecological restoration after stand-replacing wildfires. These wildfire events may be important opportunities to promote resilience to climate change, because interventions during the early stages of succession can be less costly and more effective than during later stages (Betancourt 2012). Ecological genetics, the study of genes and genotypes of natural populations in their environment, can help guide restoration efforts with the goal of promoting more resilient forests.

Research in forest genetics strives to understand the distribution and structure of genetic variation within tree species across the landscape. This information can support the development of resilient forest management strategies. Studies include examining genetic variation in adaptive traits (growth and survival) in common garden studies (Conkle 1973, Mátyás 1994, 1996; O'Neill et al. 2007, 2008; Rehfeldt 1999, Thomson and Parker 2008, Thomson et al. 2009, Ukrainetz et al. 2011), as well as using molecular genetic and genomic variation to characterize genetic variation (reviewed in Neale and Kremer 2011). Although the study of conservation genetics has been useful to the management of forest animal species (Avisé 2004), this chapter focuses on the genetics of forest trees, which are uniquely challenged in responding to climate change because they are long lived and cannot move once established, should the climate in a local area become intolerable.

An important question in forest management is how to use genetic tools to improve management responses to climate change. There are several potential strategies available to promote resilient forests. In 1992, Ledig and Kitzmiller proposed responding to climate change through assisted migration. They suggested

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moving tree seed sources uphill by an amount defined by the projected amount of increased temperature according to Hopkin's Law, which predicts that temperature goes down 1.4 °C for every 1,000-ft gain in elevation (Ledig and Kitzmiller 1992). However, they also recommended waiting 10 years before starting any program of assisted migration in order to wait until "the signal for global warming becomes clearer" (Ledig and Kitzmiller 1992: 158). This simplistic approach to responding to novel climates has been argued against, particularly given the complex nature of mountain ecosystems (Millar et al. 2007). Indeed, uncertainty in predictions of the amount of temperature and precipitation changes in mountain ecosystems is a major hurdle in designing reforestation efforts to respond to climate change (Millar et al. 2007). One suggested approach is to sow mixtures of seed sources and, hence, use a hedging approach to minimize the risk of failure (Crowe and Parker 2008, Millar et al. 2007). The topic of assisted migration (also known as managed relocation; see Schwartz et al. 2012) is highly complex, and is currently under intense debate. A recent review article describes a set of relevant ethical, policy, and ecological questions surrounding any managed relocation effort (Schwartz et al. 2012). There is currently no consensus for the use of managed relocation in managing California's forested ecosystems or in any other ecosystem (see box 3.1-2).

Forest genetics research has made a number of important contributions to land management practices in the Sierra Nevada. Perhaps none is more important than the creation of the California seed zone map (fig. 1) (Buck et al. 1970). The seed zone map indicates areas where seeds can be safely planted to preserve genetic structure and local adaptation. Forest Service silviculturists and geneticists use these seed zones to guide their seed collecting and planting decisions for ecological restoration projects that include reforestation. In California, there is one seed zone map for all tree species. The basic rule of thumb is that a reforestation project will use seeds from the same seed zone and within a 500-ft elevation band from the planting site (Buck et al. 1970). Recently, many of these reforestation projects have been organized as part of a postfire response to help facilitate the recovery of forests after stand-replacing wildfire.

Although the California seed zone map has done well in guiding reforestation efforts in the past, its future effectiveness is under question owing to projected climate change (Erickson et al. 2012). The map was created under an assumption of a static climate, and that assumption is no longer sound (IPCC 2007). New information is needed to establish best management practices for reforestation efforts in the Sierra Nevada.

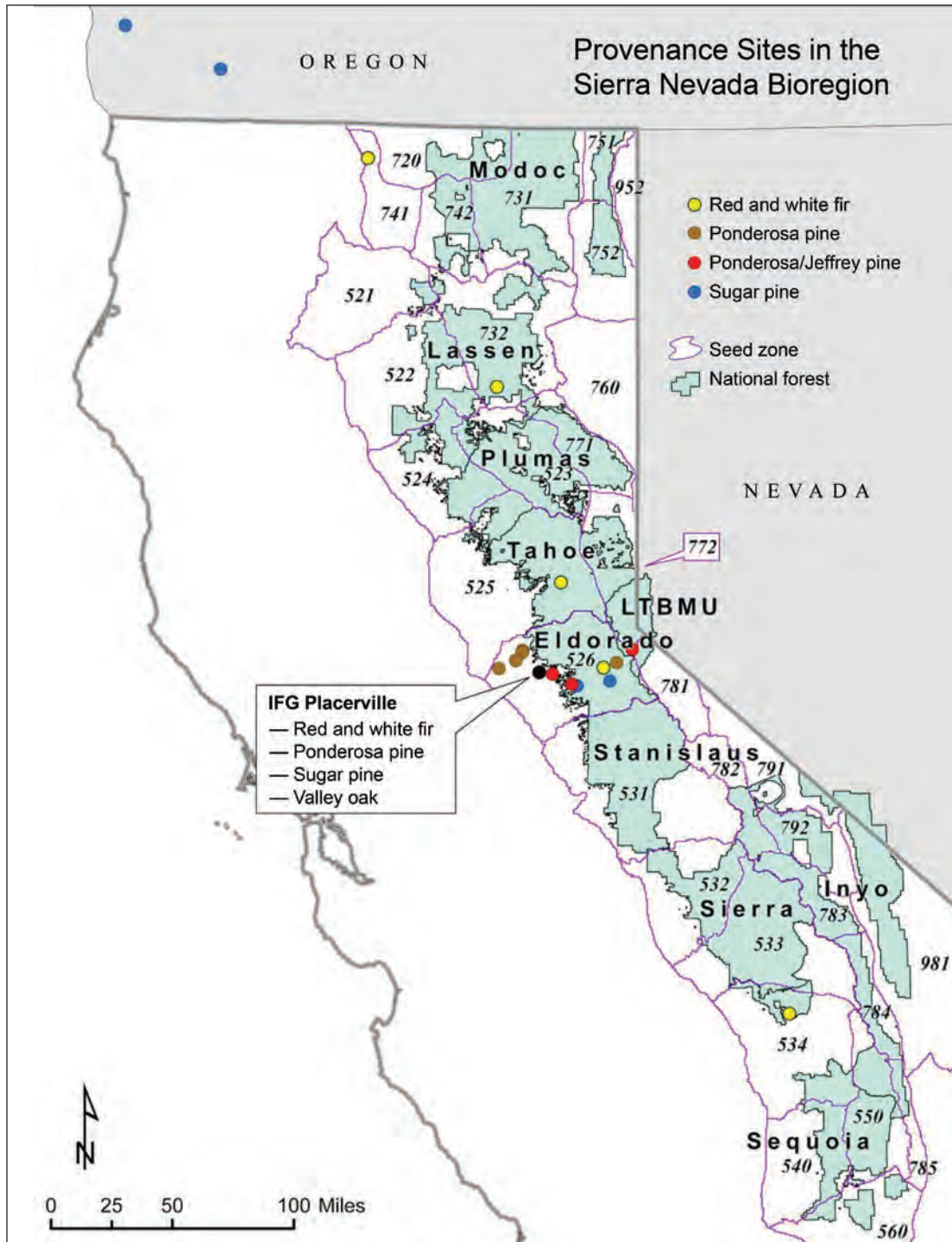


Figure 1—Seed zones (with purple outlines; the numbers identify each of the zones) and provenance tests (circles) established by the Pacific Southwest Research Station within the national forests (aqua areas) that are in the focus area of this review. The map includes two main seed zone series, 500 for the west slope and 700 for the east slope, within the Sierra Nevada synthesis area. The colored dots show locations of provenance tests in a number of conifer and hardwood species. Map by Ross Gerrard, USDA Forest Service Pacific Southwest Research Station. LTBMU = Lake Tahoe Basin Management Unit; IFG Placerville = Pacific Southwest Research Station Institute of Forest Genetics, Placerville, California.

**Box 3.1-1****Emerging Genetic and Genomic Approaches**

Recent advancements in molecular genetic and genomic approaches are making available powerful new tools, which allow for a better understanding of the genetic variation underlying important traits and the association between genetic variation and environmental variation. Recently Parchman et al. (2012) used a novel genomic approach and found 97,000 variable sites in a genome-wide survey of single nucleotide polymorphism (SNP) variation. Using a genome-wide association study, they were able to identify 11 candidate loci that were strongly associated with serotiny in lodgepole pines (*Pinus contorta*) in Wyoming. By using approaches like this, one can find the loci that are associated with ecologically and economically important traits. In addition, landscape genomic approaches are starting to identify loci associated with climate variation. For example, Eckert et al. (2010) examined 1,730 SNPs in loblolly pine (*P. taeda*) and found several of them associated with climate variables, suggesting that those loci are potentially adaptive. Association genetics and landscape genomics are beginning to provide important insights for understanding the underlying genetics of adaptive traits. Understanding how adaptive variation is distributed across the landscape can potentially help inform management decisions, including reforestation efforts.

**Provenance Tests**

Provenance tests are an important source of genetic information that can be used to inform land management. These are studies where seeds are collected from across the range of a species and grown in a common garden or gardens (ideally, multiple planting sites are used to allow a comparison between the different planting environments). Tests can be designed to focus either on variation within a species or variation among species by planting a number of different species in a single test.<sup>2</sup> Because seeds are moved from one climate environment to another, the response of each genotype to that novel climate can be measured. In general, provenance tests have revealed temperature to be the most important climate variable determining tree survival and growth (reviewed in Aitken et al. 2008). However, some analyses do show that precipitation is an important factor in determining performance (e.g., Ukrainetz et al. 2011). Interestingly, for the Sierra Nevada, predictions from

<sup>2</sup> For a recently planted current example, see <http://www.for.gov.bc.ca/hre/for/gen/interior/AMAT.htm>.

future climate models yield more consistent estimates for mean annual temperature (MAT) than for mean annual precipitation (MAP) (Safford et al. 2012). Added to that is the geographic complexity found in the mountain ecosystems of the Sierra Nevada (Millar et al. 2007). The availability of water is dependent on MAP, but also on local, microscale topography and soils, which determine what happens to rain after it falls and washes down the mountain slope. As a result, two trees growing 10 m from each other could have very different amounts of available water, but they would still be experiencing the same MAT. Clearly, even modeling current climate in a mountain environment is challenging.

An example of a very comprehensive provenance test is found in British Columbia, Canada. The Illingworth test in lodgepole pine (*P. contorta* spp. *latifolia*, *murrayana*, and *contorta*) was established in 1969, using 140 source populations, with 62 different test sites established, for a total of 69,120 seeds sown. The data from this test have been used to determine the response of populations to novel climates (O'Neill et al. 2008, Rehfeldt et al. 1999, Wang et al. 2010). Rehfeldt et al. (1999) performed a series of regression analyses to determine how the different source populations would respond to a changing climate. O'Neill et al. (2008) expanded this analysis to create a universal transfer function, which allows prediction of current and future forest productivity “for any population in any location” (page 1041) using current climate and different models of climate change. Wang

#### **Box 3.1-2**

#### **Forest Service Report on “Genetic Options for Adapting National Forests to Climate Change”**

In light of the uncertainty regarding managed relocation, Forest Service geneticists prepared a report entitled “Genetic resource management and climate change: genetic options for adapting national forests to climate change” (Erickson et al. 2012). The report presents underlying principles for the role of genetics in responses to climate change. It outlines the need for “genetically diverse and adapted seed and planting stock” (Principle 1, page 10) for ecological restoration, and it emphasizes the importance of gene conservation. The authors recommend developing seed collection, storage, and nursery capacity, particularly for a broader range of species than have historically been deployed. They also propose working to establish new provenance and common garden studies, recognizing the need for the type of data that provenance tests can generate. They also put forward the idea of examining potential in situ and ex situ gene conservation plans.



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et al. (2010) developed a universal response function (URF) using the same data, then modeled forest height for lodgepole pines in British Columbia under projected climate change scenarios, including both forests planted with local planting stock as well as planting stock predicted to have the best height growth using the URF and the A2 “enterprise” climate scenario. They found very dramatic changes between the two models, with the modeled forests planted with the “ideal” planting stock being much taller than those that used the local planting stock.

This analysis was possible because of the existence of the Illingworth Provenance Test in British Columbia. In California, there are provenance test resources established by the Forest Service Pacific Southwest Research Station for Jeffrey, ponderosa, and sugar pine, and red and grand fir (e.g., Conkle 1973; Kitzmiller 2004, 2005) (fig. 1). However, the largest number of planting sites for these tests was four—much fewer than the 62 sites used in Canada. For the provenances that were tested, similar analyses are being performed. Past analyses have shown evidence for local adaptation in both sugar pine (Kitzmiller 2004) and ponderosa pine (Kitzmiller 2005). However, with limited existing provenance test resources, it is not possible to match the level of detail that can be achieved in British Columbia for lodgepole pine. If something approaching the level of detail achieved in Canada is desired for California, investment would be needed to establish additional tests in a broader range of species, as well as across a broad range of planting sites, including those outside of traditional planting areas. The Forest Service Pacific Southwest Region has begun to establish climate adaptation plots that are designed to test the response of seedlings moving uphill within a seed zone. Plots were established within ecological restoration projects, with as much variation as possible in elevation. These sites have a great deal of potential to support future ecological restoration projects by determining how far uphill trees can be moved within a seed zone and still survive and grow; however, they will require attention over the next several decades to obtain their full value. Because these test plots were all established using material from within the same seed zone, they are not useful for testing how seeds perform in different seed zones. Although provenance tests take a long time to show results for 30-year growth in a particular climate, information can begin to be obtained from tests starting on the day they are planted. Seedling growth and survival can be assessed from the very beginning of the experiment.

It is important, however, to point out the drawbacks and limitations of provenance test data. First are the silvicultural techniques used to establish each of the planting sites. Both to reduce environmental variation and to make sure as many seedlings survive the transplanting process as possible, sites are highly prepared, and seedlings are often watered until they are well established (Aitken



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Figure 2—The Harrell provenance test in sugar pine includes 124 different sources of sugar pine, all grown in a single common garden.

et al. 2008). This can result in conditions that are very different from operational tree plantings, which often use the “plant and pray” method—seedlings are planted but not watered, and often not kept clear of competing vegetation. Another issue, particularly with historical tests, is that test sites were not established in marginal environments or outside of the range of the species (O’Neill et al. 2008). These tests were often established with silvicultural goals—finding the best seed sources for particular sites—and there was little point in learning about sites where trees did not thrive. However, under climate change, these could be some of the most important sites to include in future studies. Finally, provenance tests do not test the impacts of other important and potentially interacting factors besides climate, including fire, insect pests, or diseases (Aitken et al. 2008, O’Neill et al. 2008). A tree can be optimally adapted to grow in a certain environment, but it hardly matters if it is killed by beetles or is not resistant to a local pathogen.

## Recognition and Management of Provenance Test Sites on National Forests

As a final note, it is important that land and resource management plans recognize the significance of provenance test plots located within national forests (fig. 1). Along with other kinds of special management areas designated for research purposes, these sites are investments whose value can be lost if they are inadvertently or randomly treated without appropriate direction from the researchers assigned to oversee them. Although sites should not necessarily be deferred from treatment, if treatments are needed, they should be carefully implemented to avoid unintended impacts to the research value of the site.

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## Management Implications

There is active scientific debate about whether revegetation efforts should move beyond local sourcing of revegetation materials toward the managed relocation of genotypes that appear better adapted to expected climate change; however, there is broad consensus for using common garden experiments or provenance tests to prepare for projected conditions by better understanding how genetic variability can improve ecological restoration (fig. 3).

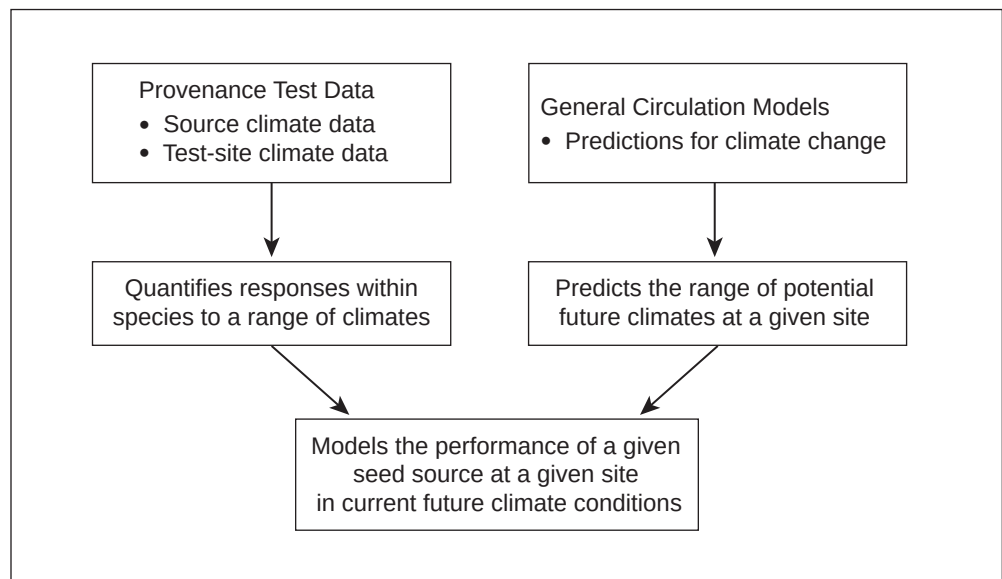


Figure 3—Flowchart illustrating how climate modeling and genetic information can help suggest seed sources to promote forests that are more resilient to climate change.

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## Glossary

**Assisted migration**—Schwartz et al. (2012) defines this as “introducing a species into a new location by bringing propagules or individuals and releasing them” (Schwartz et al. 2012: 733).

**Common garden experiment**—A study, generally in plants, that involves planting multiple sources of plants in a single common garden or across multiple gardens. When all sources of plants are planted in a garden located in their home environment as well as one or more other environments, this is called a reciprocal transplant experiment.

**Ex situ gene conservation**—Seeds are collected from trees and stored in seed banks, either for long-term conservation or later deployment as part of ecological restoration activities. Seeds from the genus *Pinus* can generally be stored in optimal conditions for many years (Bonner and Karrfalt 2008). However, other species, such as oaks, do not store well after seeds are shed, so ex situ conservation for those species requires a living gene conservation archive plantation.

**In situ gene conservation**—Populations of trees are conserved in a naturally occurring population that is part of a genetic conservation reserve.

**Managed relocation**—Schwartz et al. (2012) offers this definition: “The intentional act of moving species, populations, or genotypes to a location outside of a known historical distribution for the purpose of maintaining biological diversity of ecosystem functions as an adaptation strategy for climate change” (Schwartz et al. 2012: 733).

**Provenance test**—A type of common garden experiment, generally in trees, where sources of trees (from a set of locations or provenances) are planted in a common garden or gardens. Ideally, these provenances are from across the entire range of the species, though many studies choose to focus on a particular part of the range. All sections of this synthesis are concerned with fire because of its role as a dominant ecological process in the Sierra Nevada and southern Cascade Range. Fire has long influenced the diverse natural and cultural resources of the synthesis area, including air quality, human health, infrastructure, community well-being, soils, timber, terrestrial and aquatic wildlife, and water resources.