Chapter 4

Plant Vulnerabilities and Genetic Adaptation

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Executive Summary

The biogeography of plant species and population genetic structure within species is principally governed by climate. The association between climate change and plant distributions has been well documented since the last ice age, and recent studies have shown contemporary climate changes can create landscape-scale die-offs or movement of plant taxa. Terrestrial ecosystem conservation and restoration success hinges on understanding the vulnerabilities imposed by climate on plant taxa. Successful conservation and restoration under a changing climate will require:

- Recognizing whether climate is the root cause of changes in biotic communities.
- Determination of which species and populations are most vulnerable and at the highest risk to extirpation.
- Accurate prediction of future displacement and movement of plant communities.
- Fostering regeneration or assisting the movement of appropriately adapted plant materials.

Genetic and ecological research can provide critical components to meet these goals. GSD scientists are focusing on the following areas of research:

- Plant species-climate relationships: a means to understand how climate shapes distribution of species on the landscape. This research provides a means of predicting how species distributions could be affected by climate change.
- Adaptive genetic variation: research aimed at quantifying plant responses from different populations in a common environment. This research provides the necessary component to develop seed transfer guidelines for plant species.
- Genetic diversity and structure: use of molecular markers to identify areas of high or low diversity and how genetic variation is structured across the landscape. This research provides a means to identify physical or biological barriers to gene flow and at-risk populations with low genetic diversity.
- Ecological interactions: research aimed at identifying biological interactions critical to the success and persistence of native plants. Plant movement, either natural or human mediated, may require other organisms for pollination, seed dispersal, or seedling establishment.

Plant Species Distributions and Climate

Plant biogeography is principally governed by climate, exhibiting strong responses with both temperature and precipitation (Brown and Gibson 1983). The relationship between climate and plant species distributions has been demonstrated through several lines of research. First, contemporary predictions of plant species distributions have been shown to be highly accurate based on models using climate variables as predictors of species presence or absence (Iverson and Prasad 1998; Rehfeldt and others 2006; Friggens and others, Chapter 1 this volume). Second, past range shifts in plant distributions have been documented through patterns of genetic variation (e.g., Richardson and others 2002; Petit and others, 2003; Davis and others 2005; Richardson and Meyer 2012) and in records from packrat middens (e.g., Betancourt and others 1990; Thompson and Andersen 2000). These range shifts have been mainly attributable to climate change and associated glacial and interglacial oscillations during the Pleistocene and early Holocene. Third, studies monitoring vegetation have shown that range shifts are ongoing for a number of plant taxa and most are likely attributable to climate warming (Soja and others 2007; Beckage and others 2008; Kelly and Goulden 2008; Thomas 2010). Given this close association between climate and plant biogeography, the predicted rapid change in climate by human-made greenhouse gas emissions should be the impetus for developing the knowledge base regarding seed transfer guidelines and other activities that mitigate this change.

In western North America, climate has been implicated as a factor in recent vegetation die-offs. The drought of 2002-2003 has been associated with the widespread mortality of pinyon (*Pinus edulis*) and juniper (*Juniperus* spp.) in the southwestern United States. Breshears and others (2005) showed that this drought coincided with warmer temperatures not seen in previous droughts during the Twentieth Century. Similarly, Rehfeldt and others (2009) used weather station data to show that the changes in climate variables important in predicting aspen (*Populus tremuloides*) distribution were also associated with stands of aspen die-off caused by sudden aspen decline. As with the pinyon die-off, drought and higher-than-average temperatures in 2002-2003 have been implicated as causative factors in sudden aspen decline. Based on predictions from GCMs, the aspen die-off may represent the trigger for a range shift, wherein many of these dead or dying stands will not recover (Rehfeldt and others 2009).

While die-offs of landscape dominant plant species, such as aspen and pinyon, may represent a fundamental change in ecosystem processes, climate change could also threaten other regionally distributed or endemic plant taxa with extinction. The varied topography and soils of western North America create isolated, discontinuous patches of habitat for plant specialization. Endemics are commonly found on exposed substrates such as shale or gypsum, or are associated with cliffs or shaded slopes of isolated mountain ranges (Johnston 1977; Meyer 1986; Sivinski and others 1996). These disjunct distributions limit the colonization pathways of potential habitat in future climates, especially in plant species with limited seed dispersal capabilities. For example, environments of river canyons create one source of endemism. These microclimates with perennial water sources create hanging gardens, supporting numerous endemic plants (Welsh 1989). The persistence of these microhabitats is dependent on sustaining ground water. If droughts in these regions become more common, the hanging gardens could dry up. Another example is provided by the isolated nature of mountain ranges in the southwest. These regions support some of the highest levels of plant endemism in North America (Warshall 1995; Anonymous 2007). The Madrean Archipelago of southern Arizona, southwestern New Mexico, and adjoining states of Sonora and Chihuahua Mexico consists of some 40 isolated mountains known as "sky islands." The effects of climate change may be particularly pronounced

in these isolated ranges as vegetation zones shift upward and high-elevation habitat is lost. Bioclimatic modeling of Mexican spruce (*Picea mexicana*), which is isolated in small subalpine habitats, predicts the disappearance of contemporary habitat by 2030. However, re-emergence of suitable habitat for this species occurs 500 km to the south, a distance impossible for natural dispersal (Ledig and others 2010). Mexican spruce and other endemics will likely need human-assisted dispersal to areas of suitable habitat. To limit the vulnerabilities to climate-caused extirpation of plant taxa, bioclimatic analyses are of value in identifying new locations of suitable habitat that may emerge under climate change.

Biotic Interactions and Climate Change

In addition to direct effects, global drivers of climate change may affect plant distribution, abundance, and fitness through biotic interactions (Tylianakis and others 2008). Ecological disturbances creating large-scale plant mortality, such as insect and disease outbreaks, could be symptomatic of underlying plant stress due to climate change (Dale and others 2001). Temperature and moisture have been demonstrated to be critical components in the interaction between plants and insects or diseases, and climate change-caused stress can predispose plants to insect and disease outbreaks. However, determining whether climate change affects the intensity, geographic distribution, or longevity of an insect or disease outbreak is a complex task (Garrett and others 2006). Studies must take into account historical records of climate and outbreaks, spatial patterns of climate variables, host distributions, and other factors that affect the host and the disturbance agent interactions. Despite this complexity, some studies have shown a correlation between disturbance agent outbreaks and temperature or precipitation variability outside of the historical norms. Berg and others (2006) associated spruce beetle outbreaks in Alaska and the Yukon Territory with high summer temperatures. Likewise, Woods and others (2005) implicated climate change in an epidemic outbreak of Dothistroma needle blight. Widespread mortality of pinyon pine, previously mentioned, was further linked to outbreaks of the pinyon ips bark beetle (*Ips confuses*; Breshears and others 2005). Drought-stressed trees were unable to produce sufficient resin to ward off beetle attacks. A fungus carried by the ips may also have been a factor (P.L. Ford, personal communication).

Disruption of mutualistic relationships, such as plant-pollinator interactions, may also occur due to climate change. Many flowering plant taxa require animal pollinators for reproduction (Brantley and Ford, Chapter 4 this volume). Corresponding declines in pollinators and insect-pollinated plants have been found in northern Europe, whereas wind-pollinated plants were unaffected (Biesmeijer and others 2006). Other studies have shown that climate change could disrupt plant-pollinator interactions by changing floral phenology (Memmott and others 2007). Rising CO_2 levels and increased summer temperatures have been linked to changes in flowering phenology (Cleland and others 2007; Springer and Ward 2007; Crimmins and others 2009). Decoupling of plant flowering and pollinator availability could result in reproductive failure for both plant and pollinator. For example, flowering in ocotillo (*Fouquieria splendens*) is currently timed to synchronize with the northern migration of hummingbirds (Waser 1979). A lack of high-quality nectar resources could lead to a decline in hummingbird populations. Thus, mitigating the impacts of climate change on flowering plants that are dependent on pollinators has additional complexity and will require increased knowledge. Movement of plants to suitable habitats without recognizing the importance of pollinators could lead to failure. Other biotic interactions may also be affected, including inter- and intra-specific competition, herbivory, dispersal agents, mycorrhizae and other fungal mutualistic relationships

(Tylianakis and others 2008). The effects of climate change on these interactions have received very little attention.

Climate Change and Altered Fire Regimes

Disturbance resulting from improper grazing practices, off-road vehicle use, and other anthropogenic disturbances have contributed to the widespread invasion of exotic annual grasses, primarily *Bromus* spp. in the Great Basin and, more recently, *Bromus* spp. and *Schismus* spp. in the Mojave and Sonoran Deserts (Esque and Schwalbe 2002; Ford and others, Chapter 6 this volume). Resulting changes in wildfire regimes (shorter fire intervals and longer fire seasons) and increasing temperatures have combined to accelerate the further spread of annual and perennial exotics, deplete native seed banks, simplify community structure and species associations, and reduce landscape patchiness (Brooks and Pyke 2001; Esque and Schwalbe 2002). Ecosystem resilience declines with disruption of critical functions such as snow or water catchment, nutrient cycling, and loss of microbiotic crusts and mycorrhizae. As a consequence, the future of entire communities and their component species are at risk due to the direct impacts of wildfire and invasives, climate change, habitat fragmentation, and resulting bottlenecks to plant migration (D'Antonio and Vitousek 1992).

The status of fire-intolerant sagebrush and its communities is threatened not only by wildfire and the incursion of exotic annuals, but also by the encroachment of native conifers, in part due to fire control and northerly movement of Mojave vegetation in response to warming temperatures (Bradley 2009, 2010; Ford and others, Chapter 6 this volume). Nielson and others (2005) simulated climate change impacts on potential future distribution of the sagebrush ecosystem. The greatest warming scenario reduced the system to 20 percent of its current area within the Twenty-First Century. Currently, about 350 species of conservation concern are associated with the sagebrush ecosystem (Wisdom and others 2005) and 20 percent of the systems flora and fauna are considered imperiled (Center for Science, Economics and Environment 2002). Thus, major species losses can be expected if current trends continue.

Proposed research and management to meet these threats are: expanded research on biocontrol and other control methods for cheatgrass and other invasives (Runyun and others, Chapter 7 this volume); adaptation of native plants coexisting with invasives (Mealor and others 2004; Leger 2008), species specific seed zones (Erickson and others 2004); deployment of pooled seed sources, including accessions that will pre-adapt vegetation to expected changes in climatic conditions (Johnson and others 2010); management to reduce bottlenecks to species migration, and assisted succession (Friggens and others, Chapter 8 this volume).

Genetic Responses to Climate Change

Plant fitness, the ability to produce viable offspring, is often dependent on attunement to climate. Three types of biological responses from an organism can direct attunement: phenotypic plasticity, dispersal, and genetic change. These responses are fundamentally different biological processes occurring at different temporal scales, but all responses could potentially interact with each other and impact an organism's capacity to genetically adapt to climate change (Davis and others 2005; Visser 2008; Reed and others 2010).

• Phenotypic plasticity is defined as the capacity of a particular genotype to produce varied phenotypes in response to different environments (Pigliucci 2001). Phenotypic plasticity operates within a generation, the shortest time scale of the three responses. It can be temporary (non-heritable) or inherited through some epigenetic mechanisms,

the changes in gene expression by means other than DNA substitutions (Bird 2007). Epigenetic mechanisms could have important implications on how we assess plant vulnerabilities to climate change. For example, if a plant species possesses phenotypic plasticity in climatically adapted traits, this species may be more resilient under climate change.

- Dispersal of propagules (e.g., seed and pollen) can lead to gene flow. These dispersal processes can create a shift in gene frequencies and introduce novel genotypes from different populations, potentially affecting fitness. Dispersal occurs on a multi-generation temporal scale, yet the rate and distance propagules travel can have implications on plant species capacity to respond to a changing climate.
- Genetic change, the process of creating novel genes by mutation in the coding or regulatory DNA sequence that undergoes natural selection, occurs at the longest temporal scale. In this sense, a mutation could also include gene or whole genome duplications (i.e., polyploidy), which are common in some angiosperm lineages (Fawcett and Van de Peer 2010). These temporal scales are all dependent on the life history characteristics of the particular species. Species with short generation times will likely respond at a faster rate than those that have longer generation times (i.e., annuals are more likely to have higher fitness that perennials). Unfortunately, this benefits many invasive plant species that are annuals.

Genetic changes that affect the fitness of an organism can shape ecological processes, such as fecundity, mortality, and dispersal (reviewed in Carroll and others 2007; Kinnison and Hairston 2007). For example, a novel genotype that conveys fitness advantage to drought tolerance would increase in frequency in a climate that becomes arid, leading to higher survival, fecundity, and dispersal rates for individuals possessing this genotype. If arid conditions persist, strong selection pressure for drought tolerance could change the gene frequencies in a population over several generations. Conversely, if no drought tolerance genes exist, mortality and low fecundity could create a smaller population size. Genetic drift, stochastic changes in gene frequencies, could lead to the loss of genetic diversity, increasing the risk of extirpation of the population. A similar scenario was recently shown empirically in the flower phenology of field mustard (*Brassica rapa*). Franks and others (2007) demonstrated that flower phenology in this species responded to a five-year drought by earlier flowering and that the ancestors (i.e., pre-drought plants) had significantly reduced survival rates compared to contemporary plants.

Natural selection caused by climate is spatially dependent, especially for widely distributed species. The process can create variable plant trait responses or ecotypes across the landscape (Turesson 1925). Therefore, climatic selection has been demonstrated to be a major factor in intraspecific genetic adaptation (Langlet 1936; Savolainen and others 2007). Much of this research, completed in common garden studies of trees species, has shown that the adaptive strategies among species are not the same. For example, Douglas-fir (*Pseudotsuga menziesii*) is highly variable in growth phenology and populations have a narrow threshold for cold hardiness. The variability in this trait is mainly associated with winter temperatures and frost dates (St. Clair and others 2005). In contrast, western white pine (*Pinus monticola*) exhibits little adaptive variation to cold hardiness despite having a similar species distribution as Douglas-fir. In western white pine, cold hardiness is apparently a phenotypically plastic trait. However, for western white pine, variation in growth is strongly associated with the amount of growing season precipitation (Rehfeldt and others 1984; Richardson and others 2009). These genecological studies illustrate that ecologically similar plant species may have vastly different adaptive strategies to cope with climatic stresses and that populations within these species will respond differently under climate change.

Genetic Tools for Addressing Climate Change

Knowledge of intraspecific and population-level responses to climate change are essential for the restoration of plant species. Once associations between genetic traits and climate variables can be established, as previously discussed, genecological modeling can be used to define contemporary seed zones and predict future seeds zones using GCM scenarios (e.g., Rehfeldt and others 2002; Rehfeldt 2004; St. Clair and Howe 2007). While GCMs scenarios are not without assumptions (IPCC 2007), modeling intraspecific adaptive genetic variation in the future is instructive for identifying geographical regions of current and future on-site and off-site conservation and planning for the potential movement of desirable genotypes. However, most genecology research has been completed for forest trees and little knowledge exists for desert or species.

Molecular genetic approaches have served a different purpose to that of common garden trials of adaptive traits. Since molecular markers are generally neutral (i.e., not influenced directly by natural selection), they are valuable in assessing range-wide genetic diversity and structure. Measures of genetic diversity provide a means to assess the relative fitness of populations and the level of inbreeding (Reed and Frankham 2003). Therefore, low levels of genetic diversity suggest the effective population size is or has been experiencing a bottleneck. Further losses to population size could result in leading to a greater risk of extirpation.

Molecular markers can also reflect past biogeographic distributions and demographic changes. Isolated populations from past glacial cycles are often inferred from patterns of genetic variation. Therefore, molecular markers are indirectly tied to past climate events. For example, organellar DNA markers were used to elucidate putative glacial refugia and post-glacial colonization in whitebark pine (*Pinus albicaulis*). Richardson and others (2002) showed that Holocene warming provided whitebark pine with opportunities to establish contact zones and genetic introgression from previously isolated populations. Other studies have shown that present-day genetic patterns are supported by bioclimatic modeling of predicted Pleistocene climate (Rebernig and others 2010). Much of the research using molecular markers on temperate plants show similar patterns of post-glacial colonization, such that the higher proportions of genetic diversity and structure are found in the lower latitudes of a species' distribution (Hampe and Petit 2005). The skewed distribution of genetic diversity may make species more vulnerable to climate warming since lower latitude populations are generally at higher risk of extirpation.

Popular population genetic techniques such as microsatellites and amplified fragment length polymorphisms have been instrumental in identifying vulnerable plant taxa and populations by elucidating genetic diversity and structure. However, these techniques have limitations in the amount of detectable genetic variation and applications to other areas of genetic research. Next-generation sequencing technology has the capacity to sequence millions of 50 to 500 base pair fragments of genomic DNA or RNA that can uncover hundreds of thousands of single nucleotide polymorphisms (Mardis 2008). Researchers can develop these polymorphisms into thousands of molecular markers for discerning genetic relationships. The capabilities of next-generation sequencing have been compared to existing data generated from traditional sequencing methods in Fishers (*Martes pennanti*). Knaus and others (2011) discovered distinct populations of this rare carnivore in California that was unresolved in the previous genetic data. Such findings will a have an impact on how this species will be managed. In addition to providing more accuracy in discerning genetic relationships, next-generation sequencing offers greater versatility to address questions in plant-climate interactions.

Two different molecular approaches have the capability to elucidate the relationships between genotype and phenotypes, bridging the gap between physiological/phenotypic plant responses and the underlying genotypic mechanisms.

- RNA sequencing: a process of transcriptome profiling (i.e., sequencing all expressed RNA transcripts in a sample) using next-generation sequencing technology. In this approach, RNA sequences are decoded and levels of gene expression can be estimated by transcript copy number (Wang and others 2009)
- Association genetics: an approach to identify a gene or genes involved with a phenotype by determining a pattern of presence and absence between molecular markers and a trait using groups of plants or plant populations with differing phenotypes (Neale and Savolainen 2004; Ingvarsson and Street 2010)

Research involving next-generation sequencing can improve our understanding of processes and mechanisms involved with creating variable traits and physiological responses important to climatic adaptation.

Potential Plant Vulnerabilities

Based on the available research and the previous discussion, inferences can be drawn about the general plant characteristics that may increase vulnerabilities to climate change. While the details on criteria for assessing and scoring vulnerabilities are discussed elsewhere (Friggens and others, Chapter 8 this volume), we provide a list of characteristics that are potentially influential to the success or failure of plant species under climate change.

- Habitat specialists: Many habitat specialists and narrow endemics could be at high risk to climatic extirpation. Examples include the hanging garden flora previously discussed. These plants species are limited in their movement because similar habitats are rare or nonexistent. For managers, long-term seed banking may be the only option for preservation of these species.
- Plant dependencies on other organisms: Plants that rely on other organisms for their reproduction (e.g., pollinators and seed dispersers) or survival (e.g., mycorrhizal fungi) could be more vulnerable to climate change (Brantley and Ford, Chapter 3 this volume). Understanding the relationships of these plants and their associates is an important step to increase the chances for successful restoration or movement of plant species.
- Life history characteristics: Generation time, fecundity, and dispersal capabilities are important life history characteristics when considering vulnerability. Species with long generation times, low seedset, and limited dispersal capabilities are typically vulnerable to climate change. Unfortunately, these life histories also describe many of our nativet species (Runyon and others, Chapter 7 this volume).
- Adaptive genetic strategies: Plants have different adaptive genetic strategies. Plants that have more narrowly defined adapted populations will require more attention to the movement of seed to the appropriate seed zones. Therefore, plants with narrowly defined adapted populations are more likely to experience maladaptation with climate change.
- Genetic diversity: The extant genetic structure and diversity within a species can be a major influence on vulnerability to climate change. Genetic diversity affects a spectrum of adaptive responses a plant species can possess. Therefore, reduced diversity could impact fitness, making a species more vulnerable to climate change.

Table 4-1. Research areas for mitigating climate change impact on grassland, shrubland and desert ecosystems of western North America.

Research focus	Details	Benefits
Bioclimatic modeling	Assessment of which climate variables can be important to species distributions based on presence/absence data (Friggens and others, Chapter 1 this volume)	Predicts current and future species distributions
Genecological modeling	Intraspecific genetic relationship with climate	Used to develop current and future seed zones
Climate/disturbance interactions	Relationships between disturbance agents (insects, disease, fire) and climate (Ford and others, Chapter 6 this volume)	Key to elucidating climate interaction with disturbances
Climate/invasives interactions	Understanding relationships between invasive species, natives, and climate change (Runyon and others, Chapter 7 this volume)	Offers insights into how climate affects invasive species interactions with natives
Autecology/climate relationships	Climate impacts to breeding systems, seed dispersers, and pollinators (Brantley and Ford, Chapter 4 this volume)	Identifies unseen vulnerabilities with pollinator/dispersal agents
Molecular genetics	Use of DNA or other markers to assess intraspecific genetic structure and diversity	Identifies unique populations and areas of high genetic diversity

Research Needs

The impacts of climate change on the flora inhabiting grassland, shrublands, and desert ecosystems of western North America remain largely unknown. Accurate assessments of plant species' potential vulnerabilities to climate change hinge on research needs spanning multiple disciplines to resolve their complexity (table 4-1). Understanding of these vulnerabilities can then be developed into plans and technologies for conservation and restoration (Friggens and others, Chapter 8 this volume). At the heart of these complex problems are several key principals: (1) recognizing changes in plant species and communities and whether or not climate is the root cause, (2) understanding species vulnerabilities under climate change, (3) accurate prediction of the movement of plant communities to plan for the future, and (4) mitigating these changes by fostering regeneration or assisting the dispersal of appropriately adapted plant materials.

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