Chapter 4. Using the Southwest Experimental Garden Array to Enhance Riparian Restoration in Response to Global Environmental Change: Identifying and Deploying Genotypes and Populations for Current and Future Environments

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Introduction

The role of genetics in ecosystem restoration has largely revolved around the policy of using local genotypes (i.e., those sourced from areas near the restoration site), based on the logic that local plants are best adapted to local conditions (Johnson et al. 2004; Meffe and Carroll 1977). In a relatively stable environment, this is a sound practice; however, global environmental change impacts on the landscape are increasingly rendering this policy as inadequate at best and damaging at worst (Whitham et al. 2010). Here we define "global change" as ongoing changes in temperature, moisture, interactions with invasive plants and pathogens, increases in the frequency and severity of environmental extremes (e.g., fires, droughts), and other challenges (Cayan et al. 2010; Gutschick and BassiriRad 2003; Jones and Monaco 2009). Because of rapid environmental change, plants that are locally adapted to current environmental conditions are likely to become increasingly maladapted to their changing native environments. For example, in Arizona, Grady et al. (2011, 2015) found that Fremont cottonwoods (*Populus fremontii*) were currently locally adapted along an elevational gradient, and that tree genotypes from lower elevations transplanted to higher elevations were predicted to outperform the local genotypes at higher elevations under climate change conditions. In regions of especially rapid change such as the American Southwest (Garfin et al. 2013; Seager et al. 2007), local populations are likely to lack sufficient genetic variation to adapt to these new environments (Aitken et al. 2008; O'Neill et al. 2008a). Similarly, with the rapid velocity of climate change coupled with fragmented landscapes (Loarie et al. 2009), many species cannot migrate fast enough to reach favorable environments (Aitken et al. 2008; Davis and Shaw 2001).

Ignoring the reality of global change sets up restoration efforts for failure. Given that most restoration projects focus on foundation plant species that, by definition (Dayton 1972), shape the communities and ecosystems around them, discounting global change impacts to these foundation species will also lead to high biodiversity loss and altered ecosystem function. Failed restoration projects could also result in the loss of future restoration funding. Riparian and aquatic ecosystems support some of the highest biodiversity worldwide, and incorporating future climate change impacts in the restoration planning process is essential for successful preservation of these valuable habitats and the wealth of species they support. These problems are recognized as a global issue that affects riparian and aquatic organisms worldwide (Davies 2010).

Robust experiments are a key component of identifying which species, populations, and genotypes are most likely to survive both current and future environmental conditions. Just as agricultural field trials have been essential for crop improvement, the same basic field trial approach is being used for forest trees and other species in wildlands (e.g., Marris 2009; O'Neill et al. 2008a). In the American Southwest, we have established field trials of riparian cottonwoods and willows that are embedded within larger landscapes to be restored. We recommend such field trials as a first step in restoration to minimize future risks and enhance project success on adjacent lands.

The Southwest Experimental Garden Array (http://www.sega.nau.edu) was specifically funded by the National Science Foundation to develop this approach. Established along a 1,400-meter elevational gradient, the SEGA gardens allow researchers and managers to understand predicted climate change impacts across five major vegetation zones in Arizona. Based on findings quantified in gardens (Evans et al. 2016; Grady et al. 2011, 2015) and in the wild (Ikeda et al. 2017), restoration biologists can deploy genotypes from populations that show adaptive potential and are most likely to survive in a changing environment. In so doing, both the foundation species and the diverse communities they support can be preserved for future generations (Ikeda et al. 2014).

The following sections develop the logic of this approach. We: give evidence that global change results in maladaptation; emphasize the importance of focusing first on foundation plant species that are the community and ecosystem drivers; describe experimental approaches that can be used to identify adapted genotypes for use in restoration; and discuss the importance of maintaining high genetic diversity for the evolutionary potential and highest biodiversity of foundation species' communities.

Local Adaptation in a Stable Environment and Maladaptation with Global Change

Many studies show that plants are generally locally adapted to their environment (e.g., Clausen et al. 1940; Hereford 2009; Joshi et al. 2001; Savolainen et al. 2007). Thus, the demonstration of local adaptation is a primary justification for using only local stock in restoration, which is the current practice for restoration within most national parks. However, climate change and other global change stressors such as invasive species, drought, and other extremes are causing dramatic shifts, such that locally adapted plants are becoming increasingly maladapted (Jones and Monaco 2009). This decoupling of plants from the environments they were adapted to is resulting in landscape-level die-offs (Allan et al. 2010; Gitlin et al. 2006; van Mantgem et al. 2009) and a shift in the elevational and/or latitudinal distributions of species to environments that match the site conditions of their former home environments (e.g., Allen and Breshears 1998; Brusca et al. 2013; Chen et al. 2011; Walther et al. 2002).

A mismatch between the environments that species are currently adapted to and what the environment has or will become in the future is illustrated in figure 6, showing a photograph of the Bill Williams River that is suffering from upwards of 85 percent mortality of Fremont cottonwood. This mortality is associated with an ongoing drought that began about 5 years prior to a high mortality event that first became evident in the summer of 2015. Concurrent with this mortality event was a lack of surface stream

Figure 6—Photo of cottonwood riparian forest taken March 28, 2017, along the lower reaches of the Bill Williams National Wildlife Refuge in Arizona. Photo by co-author Hillary Cooper.

flows, a water table that had receded below 5 m, and an increase in extreme summer temperatures events ≥ 50 °C. These conditions have continued through the present (September 2017) and are associated with continuing mortality. High mortality of these foundation trees is of great concern since this forest is home to many sensitive and listed species (e.g., Lower Colorado River Multi-Species Conservation Program: LCR-MSCP 2004).

As such drought conditions persist or worsen into the future as species distribution models predict for the Sonoran Desert ecotype of *P. fremontii* (Ikeda et al. 2017), restoring with local stock would likely result in restoration failure for both the cottonwood and its many dependent species. Similar forecasts are predicted for many forest trees throughout western North America (Rehfeldt et al. 2006). Thus, experimentally identifying source populations and genotypes from non-local stocks that can survive both current and future conditions is crucial for restoration projects to be successful. Furthermore, when local plants are no longer locally adapted as figure 6 emphasizes, concerns about genetic pollution are largely negated. The focus should shift toward finding stocks that can survive in altered environments and simultaneously maintain the listed and sensitive species that depend upon this habitat for their survival (e.g., Bangert et al. 2013).

The Importance of Focusing on Foundation Species

Riparian foundation species such as cottonwoods and willows support hundreds of other organisms including sensitive and listed species (e.g., Bangert et al. 2013; Patla 2014; Skagen et al. 2005). Therefore, a first priority should be to identify the foundation species that play a central role in defining their respective communities and ecosystems and focus on their preservation as a first priority (Dayton 1972; Ellison et al. 2005; Whitham et al. 2003). Furthermore, many studies have shown that different plant genotypes support different communities and ecosystem processes (Crutsinger 2016; Lamit et al. 2015; Whitham et al. 2012). The communities that these different genotypes support represent a heritable plant trait (Gehring et al. 2017; Keith et al. 2010; Shuster et al. 2006). Thus, it is essential that we consider preserving not only species, but also the intraspecific genetic variation within these species. High genetic diversity in foundation species drives higher biodiversity in their associated communities and enhanced ecosystem processes (e.g., Ferrier et al. 2012; Fischer et al. 2014; Wimp et al. 2004). Thus, the problem of conserving riparian communities (and other vegetation types) is three-fold:

- Preserving foundation species.
- Preserving the genetic diversity of foundation species essential for maintaining their adaptive potential and role as a foundation species supporting diverse associated communities and ecosystem processes.
- Understanding the relative importance of genetics versus the environment and how they interact (G x E interactions) to affect foundation species, associated communities, and ecosystem processes.

To achieve these three goals in a changing environment, we must identify the individual plant genotypes and populations that can survive both current and future environmental conditions for a given restoration site (Grady et al. 2011; Ikeda et al. 2017; O'Neill et al. 2008a) and identify the corridors that maintain gene flow among populations as landscapes become more fragmented (Bothwell et al. 2017) and may suffer from the loss of genetic diversity (Vranckx et al. 2012). By focusing on these foundation species that are community and ecosystem drivers, we can also save many other species that are dependent upon the critical habitat they provide. In the next section, we describe how we can rigorously and experimentally identify the populations and genotypes of foundation species most useful in restoration.

Quantifying Which Stocks Will Survive Future Environments

Experiments are essential for identifying which species, populations, and genotypes are most likely to survive both current and future environmental conditions. The basic experimental approach pioneered by Clausen et al. (1940) is to establish field trials on portions of lands that are slated for restoration. Because the findings from field trials are most valid for the biotic and abiotic environment in which they are measured, having these sites embedded in larger restoration sites ensures that the findings from the field trials have the same soils, communities, and other variables that are most relevant to the adjacent sites to be restored. Based on quantification of plant performance (e.g., survival, growth, biodiversity, community stability, ecosystem functions) from such field trials, managers can identify stocks that exhibit adaptive potential to changing environments so they can be used to restore adjacent lands. This approach maximizes both short- and long-term plant performance goals and reduces risk of failure. Field trials have long been a standard practice in agriculture for maximizing yield, but they are much less common in wildlands restoration that necessitate more complex metrics of success (e.g., biodiversity, ecosystem services). Long-term monitoring of these field trials is especially important with long-lived species, as genotypes that do best in the short term may exhibit higher relative mortality in the long term or vice-versa (e.g., Sthultz et al. 2009).

Just as agricultural field trials have been essential to identify superior genetic lines to maximize crop yield under current and future conditions, the same basic field trial approach is being used with commercially important forest trees (e.g., Marris 2009; O'Neill et al. 2008a,b). As an example of the success of this approach, O'Neill et al. (2008a) developed a model using a network of provenance trials to match seed source populations of lodgepole pine with planting sites where they will perform best under future climatic conditions. Based on their findings, it is now reforestation policy in British Columbia to plant with trees adapted to a 2 °C hotter environment than the local stock (Marris 2009; O'Neill et al. 2008b; Pedlar et al. 2011), and these recommendations are being further refined to obtain even better matches with projected future environments (O'Neill et al. 2017).

Research in the United States on foundation tree species has greatly benefited from this field trial/common garden approach, exemplified in a new research facility, the Southwest Experimental Garden Array (SEGA). The provenance trial approach specifically involves collecting genotypes from each of several different populations throughout a plant's range and reciprocally transplanting them in common garden test sites to quantify their performance in different environments. Northern Arizona University (NAU) has undertaken a long-term program to develop SEGA as a research platform to study and provide solutions for utilizing genetics-based approaches to mitigate climate change, invasive species, and other global challenges. This research platform (fig. 7) allows collaborating scientists and institutions (e.g., USGS, USFS, NAU) to quantify the ecological and evolutionary responses of species to changing climatic conditions using emerging technologies.

SEGA was initiated in 2012 with $4.5 million in seed funding from the National Science Foundation (NSF) and NAU to create a network of 10 gardens along an elevation gradient in northern Arizona. The SEGA model is flexible, and a growing network of satellite sites are being added by users that expand upon and increase the resolution of the core sites. Because data are archived to NSF standards and are available online, this array is ideally suited to the experimental study of gene by environment interactions that can best be addressed using a common garden network. Study organisms span from soil microbes, grasses, forbs, shrubs, and trees.

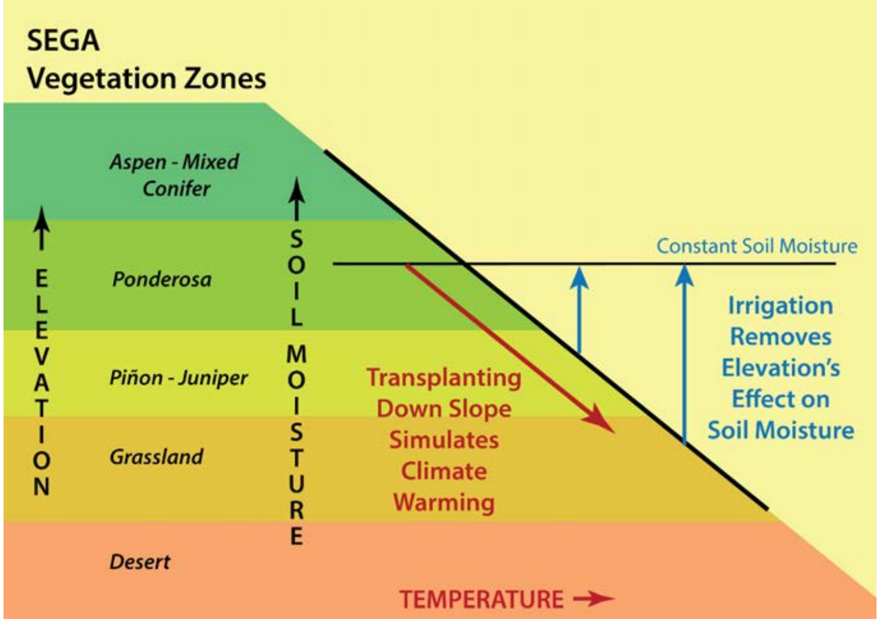


Figure 7—The Southwest Experimental Garden Array (SEGA) spans a steep elevational gradient of 1,400 m in northern Arizona that encompasses desert to aspen-mixed conifer vegetation types. Each site has irrigation to help establish plants and experimentally eliminate the effect of soil moisture with increasing elevation if desired. A weather station at each site, sensor arrays, live video, and other instrumentation allow researchers to monitor their plots remotely from their home institutions. Illustration by Paul Heinrich from the SEGA website http://www.sega.nau.edu.

Because temperature and moisture predictably change with elevation, these common gardens arrayed along an elevation gradient reflect climatic differences from desert to aspen-mixed conifer forest biomes that mimic the effects of climate change. Thus, this elevation gradient allows researchers to simulate the effects of climate change. For example, by planting the same genotypes of plants in multiple gardens, especially at lower elevations where it is hotter and drier, plants can be challenged with expected future climatic conditions. Researchers can then identify genotypes that show adaptive potential consistent with survival in a changing environment for use in restoration. Similarly, by adding supplemental water at a site or removing water with the use of rainout shelters, researchers can quantify the combined effects of temperature and moisture gradients with even greater control, or quantify just the effects of temperature alone. Experimental separation of temperature and moisture effects is especially important since increasing temperature has been demonstrated in virtually all climate models, while precipitation predictions are more variable as some areas might get wetter or have a change in the distribution of precipitation.

In combination, this experimental design allows researchers to identify optimal populations and genotypes that will perform best on adjacent restoration sites. Experimental designs also allow more complicated studies to include the examination of nurse plant effects and mycorrhizal mutualists (e.g., Gehring et al. 2017), the planting of co-adapted communities (i.e., multiple species co-evolved at the same site) planted and tested together versus randomized plantings of species from different sites (Grady et al. 2017), and planting of genotypes to promote biodiversity, community stability, and network structure (Keith et al. 2017).

SEGA enables a new generation of genetics-based climate change research that allows researchers from diverse disciplines to quantify the ecological and evolutionary impacts of climate change on (1) foundation plant species, (2) their associated communities, (3) native-exotic species interactions, and (4) the ecosystem processes that emerge from these interactions. Additionally, the Northern Arizona Research Greenhouses support plant propagation for use in SEGA, and the Environmental Genetics and Genomics center (EnGGen) allows researchers to genetically characterize their target species and identify candidate genes for functional traits of special interest (e.g., drought and temperature tolerance, productivity). These integrated facilities greatly enhance the research potential of SEGA.

In short, SEGA and related facilities allow unprecedented opportunities to address issues important in riparian systems, and other vegetation types, that can enhance restoration success for future climates and other global challenges. SEGA emphasizes interdisciplinary-interagency collaborations, which can help shorten the turn-around time between discovery and implementation by land managers.

SEGA sites have provided important findings that can be used by restoration biologists and managers to select high performing tree genotypes for a given restoration site under future conditions. For example, using trees collected from 14 source populations of Fremont cottonwood and grown at a Bureau of Reclamation riparian restoration site on the Lower Colorado River (fig. 8), Grady et al. (2011) showed that different genotypes and populations of Fremont cottonwood predictably varied in their performance when grown at the lower edge of their distribution where record temperatures can exceed 50 °C. From these studies, five major findings emerged:

(1) Transfer distance has an important impact on annual above-ground net primary

productivity (ANPP). A transfer distance of 6.5 °C means that a high-elevation, cool-site population was transferred to the warmer, low-elevation field trial, and the greater the transfer distance, the greater the decline in ANPP (fig. 8). ANPP is important because it reflects the growth rate of individual tree genotypes, but it is also positively correlated with survivorship (Grady et al. 2015) and biodiversity (Ikeda et al. 2014; Stone et al. 2010; Swaty et al. 2004). Comparing the same genotypes from different transfer distances further revealed that local populations had genetics-based leaf economic traits that made them adapted to the local site (Grady et al. 2013).

(2) Lower elevation source populations are currently better adapted to temperatures that can exceed 50 °C than higher elevation populations where temperatures are cooler. This finding of local adaptation is supported by the fact that populations like the low-elevation field site on the Lower Colorado River (i.e., sites that have a long, hot growing season) achieve higher ANPP than populations from higher mountain populations (i.e., sites that are genetically adapted to frost and a shorter growing season; fig. 8). However, with ongoing and projected climate change, local stock is expected to become maladapted.

(3) The slope of the regression line shows the sensitivity of cottonwoods from the source populations used at the planting site to temperature (mean annual maximum temperature, MAMT) (figs. 8, 9). Foundation species characterized by high sensitivity (i.e., with a steep regression slope) are key candidates for conservation/restoration strategies because of their sensitivity to climate change. Less sensitive species with a shallow regression slope might receive lower priority (Grady et al. 2011). In other words, populations of species with a more shallow regression slope can be transferred greater distances without suffering a loss in productivity compared with populations of species with a steep slope.

(4) The trait-based variance of growth is illustrated by standard error vertical bars in figure 8, which represents a population's potential to adapt to climate change. Thus, for any population shown in this figure, if the predicted change in climate is less than the variance, then the population has the potential to adapt (evolve) to predicted changes. Such rapid evolution has been demonstrated in pinyon pine (Sthultz et al. 2009). After the record drought in 2002 that resulted in landscape-level mortality, the genetic composition of the survivors was significantly different than the populations prior to the drought; similar findings have been found with other plants in response to rapid climate shifts (e.g., Franks et al. 2007) and introduced mammalian herbivores (Smith et al. 2015).

Populations with high genetic variation in climate change related functional traits allow rapid evolution to new conditions. However, if predicted climate changes exceed the genetic variation in a population's climate change related functional traits, then that population is likely to die out once conditions exceed the ability of all members to cope with the hotter environment. In other words, the pace of climate change leaves little room for adaptation beyond existing genetic variation. Thus, in regions of the world where global change is highest, it would be a grave mistake to depend upon rapid evolution to solve this problem; once the trait variation in a population is exceeded (e.g., temperature or drought tolerance), the local population will likely be extirpated. Genotypes already adapted to a hotter environment represent the logical source of stock for long-term restoration in an altered environment. Thus, if the temperature of the planting site is projected to increase by 2 °C, source populations already adapted to sites that are already 2 °C warmer than the planting site would be good sources of propagation stock.

Figure 8—At a low elevation site at the lower edge of the distribution of *P. fremontii,* mean Aboveground Net Primary Productivity (ANPP) per population is plotted as a function of the temperature transfer distance of the source population to the restoration site. A transfer distance of 0 °C indicates a source population from a hot site similar to the hot planting site at low elevation. A transfer distance of 6.5 °C indicates a cooler, high elevation mountain population transferred to the hotter, lower desert planting site and a mismatch in environmental conditions that each population is locally adapted to (adapted from Grady et al. 2011).

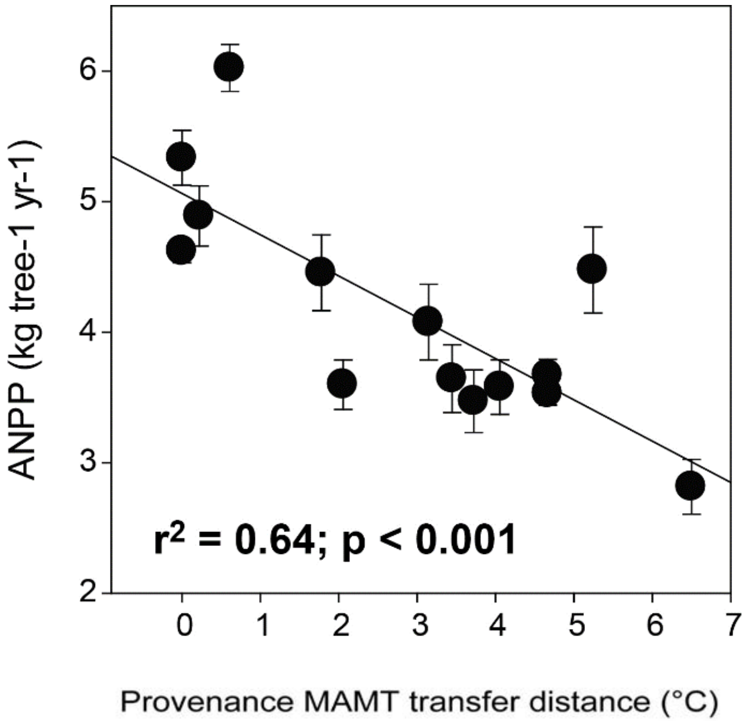
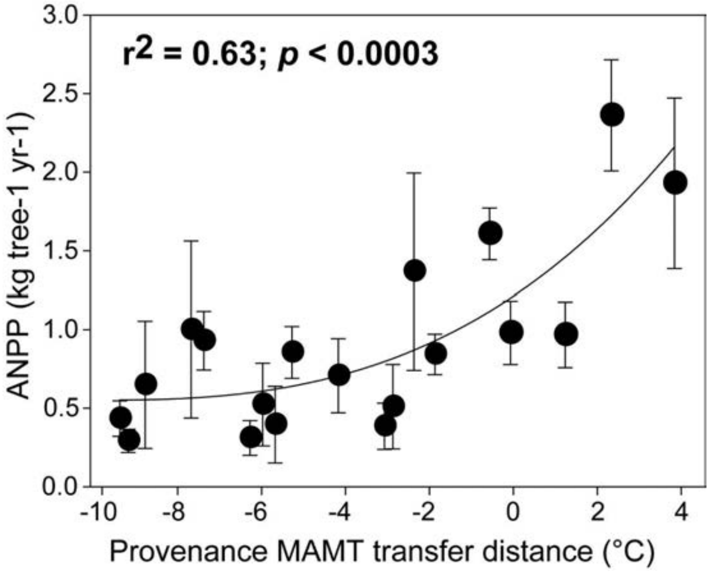


Figure 9—At a high elevation site nearer the upper, cold edge of the distribution of *P. fremontii,* mean Aboveground Net Primary Productivity (ANPP) per population is plotted as a function of the temperature transfer distance of the source population to the restoration site. A transfer distance of 0 °C indicates a source population from a cooler site similar to the cooler planting site at high elevation. A transfer distance of -10 °C indicates a hotter, low elevation population transferred to the cooler, higher elevation planting site and a mismatch in environmental conditions that each population is locally adapted to (adapted from Grady et al. 2015).



The problem of identifying which populations to use in restoration is especially grave at the lower edge of the species' distribution, because there are no other populations that are currently known to exist in even hotter environments. In other words, managers may have few options for finding individual genotypes or populations that are already adapted to what the environment will become in the future. This suggests that efforts to restore cottonwoods at the lower edge of their distribution are likely to fail with further climate change that exceeds the physiological tolerances of the species that would be reflected in widespread mortality and recruitment failure. In such cases, researchers and managers should use field trials to identify and experimentally deploy the most functionally equivalent species that is adapted to an even hotter environment to potentially fill the functional role of cottonwood as a foundation species (e.g., perhaps mesquite). Although not a preferred solution, this may be the best option available to achieve some restoration goals of supporting community biodiversity and providing ecosystem services.

(5) While the options for lower elevation edge populations facing climate change may be limited due to a lack of genetically appropriate stock, higher elevation populations have more promising options, because there are numerous populations at lower elevations that are already adapted to a hotter environment. For example, in another field trial study conducted near the upper end of the elevational distribution of Fremont cottonwood, Grady et al. (2015) demonstrated local adaptation in which high-elevation populations outperformed low-elevation populations in the high-elevation garden (fig. 9). With projected climate changes, these high-elevation populations would also be expected to become maladapted to the new environment. Because numerous populations live at lower elevations with a hotter environment, managers have the opportunity to select among these populations to find the one(s) that are the best candidates to plant at a higher-elevation site undergoing climate change, by considering both transfer distance that equates with projected warming as well as similarities in site characteristics (e.g., soils).

Using the information in this graph, we can select source populations for a predicted level of climate change. For example, if temperature is predicted to increase by 3 °C at the high-elevation planting site, using the empirical data from this graph, populations from lower elevation sites that have evolved for a 3 °C hotter environment should do best in the hotter future environment of the high-elevation planting site (see -3 °C populations indicating a hotter to cooler temperature transfer distance of 3 °C). Given our findings, we recommend a maximum 3 °C transfer distance to balance success between current and future climates. While trees from greater transfer distance would be better adapted to even hotter environments, trees would suffer from productivity losses in the current cooler environment. However, transfer distances of ≤ 3 °C would suffer minimal productivity losses in the current environment and would perform best in a 3 °C warmer future environment. If climate change is projected to increase by 6 °C, a phased or stepwise approach over time is recommended, in which increasingly more temperature tolerant genotypes and populations are planted as the climate continues to change.

In combination, these findings provide powerful tools to assist managers in the selection of genotypes and source populations that can survive a given level of climate change. Based upon the above and other studies, we recommend planting a combination of local stock for the current environment and stock from sites that are 1-3 °C hotter than the planting site, which would perform best in predicted future climates. The combination of these genotypes and populations provides important genetic variation that selection can act upon as climate change and other stressors determine who wins and who dies. Such strategies are especially important in regions where global changes are great such as the arid Southwest.

Insistence on using only local stock—where the mismatch of the local populations and genotypes with the new environment are great as in figure 6—greatly diminishes the probability of successful long-term restoration. We emphasize that field trials should be embedded in the sites where extensive restoration is proposed because they standardize soil conditions, community species pools, and other factors that could confound planting strategies based upon findings from sites farther removed from the actual restoration site.

The Importance of Maintaining Genetic Diversity for Associated Communities

We emphasize that restoration plantings must maintain high genetic diversity both for the foundation species as well as their associated communities. Genetic variation provides the essential building blocks for natural selection to act upon (Fisher 1930), thereby allowing species to evolve in response to unforeseen challenges including future climate change, new invasive species, and currently unknown biotic and abiotic effects.

For example, Sthultz et al. (2009) documented rapid evolution in pinyon pine, *Pinus edulis,* in response to record droughts, in which drought-tolerant genotypes suffered only 21 percent mortality, whereas drought intolerant genotypes from the same population suffered 68 percent mortality resulting in a rapid shift in the genetic structure of the population. Without such genetic variation naturally occurring in the population, the impacts of drought could have been much more severe, resulting in a major bottleneck event and potential local extinction had all genotypes been drought intolerant. These and other studies clearly demonstrate the importance of maintaining high genetic variation in foundation species populations, even when the roles of genetics in community diversity and the environmental conditions likely to favor certain foundation species traits are poorly understood.

For example, Orians and Fritz (1996) showed that under one set of environmental conditions, one group of willows was found to be resistant to insect herbivory, but under another set of environmental conditions, another group of willows was most resistant to insect herbivores. Similarly, antagonistic pleiotropy refers to a single gene controlling many traits, with at least one trait conferring positive fitness effects and at least one resulting in negative impacts to the organism (Yanchuk et al. 2011). For example, a plant may exhibit suboptimal performance under normal environmental conditions, but outperform the “optimal” genotypes under conditions of extreme stress. Planting only the most productive genotypes tested under “normal” conditions could result in large losses under drought conditions. In other words, high genetic variation is an insurance policy against unknown future biotic and abiotic conditions.

In addition to high genetic diversity being crucial for the long-term survival of foundation and other species, many studies have also demonstrated that high genetic variation in foundation species promotes greater biodiversity in their associated communities (e.g., Ferrier et al. 2012; Crutsinger et al. 2006; Wimp et al. 2004). A primary reason for this relationship between genetic diversity in the foundation species and the diversity of the associated community is that different genotypes support different communities. Because many plant traits such as phenology, phytochemistry, growth, and morphology have a strong genetic component and can covary and interact with each other (Endler 1995), the combination of all these traits is referred to as the multivariate phenotype (Holeski et al. 2012). As this multivariate phenotype differs greatly among individual genotypes, it is not surprising that different organisms and communities are found on different plant genotypes and that interspecific indirect genetic effects (IIGEs) among species in a community further lead to differences in community assembly on different plant genotypes and evolution (Allan et al. 2012).

Because these multivariate plant traits and interactions are genetically based and passed to their offspring, the communities they support represent heritable traits that can be quantified (Keith et al. 2010; Shuster et al. 2006). Numerous studies of plants around the world from the tropics to the tundra and desert to alpine environments exhibit community heritability in which related individuals tend to support the same communities (review by Whitham et al. 2012). Numerous studies with cottonwoods have demonstrated the importance of individual genotypes supporting different communities of diverse organisms including mycorrhizal mutualists, decomposing soil fungi and bacteria, lichens, twig endophytes, and insects that are closely tied to the multivariate phenotypes of individual plant genotypes (Lamit et al. 2015).

Studies of other systems such as conifers and eucalypts have shown similar patterns. Gehring et al. (2014) showed that different genotypes of pinyon pine (*Pinus edulis*) supported different mycorrhizal communities, and Barbour et al. (2009) showed that different genotypes of blue gum (*Eucalyptus globulus*) supported different communities of arthropods and fungi. These genetic effects even extend to beavers (Bailey et al. 2004), elk (Bailey et al. 2007), nesting birds (Martinsen and Whitham 1994) and seed-eating birds and mammals (Christensen and Whitham 1993). Thus, if maintaining high biodiversity is desirable, managers can select for a combination of different genotypes and populations that support the greatest biodiversity.

Another important principle is the concept of managing foundation species for both genetic and community connectivity. Genetic connectivity considers the degree to which populations of foundation species share genes and associated alleles across their distribution. Similarly, community connectivity considers the degree to which populations of foundation species share communities across their distribution, which is a concept supported by the genotypic-community associations described above. Thus, it is critical to understand the biotic and abiotic factors that either facilitate or inhibit genetic connectivity in foundation species and how it may change over time in conjunction with environmental change.

Cushman et al. (2014) and Bothwell et al. (2017) recently demonstrated the utility of this approach via the identification of genetic corridors in two widely distributed foundation species, *P. fremontii* and *P. angustifolia.* Like many cottonwood species, both *P. fremontii* and *P. angustifolia* support large and diverse communities of organisms whose connectivity may depend, in part, on the maintenance of genetic connectivity in their respective foundation species. Although such studies are in their infancy, "managing for connectivity" in both foundation species and their associated communities constitutes a "best approach" for preserving biodiversity into the future.

In combination, maintaining high genetic diversity in restoration plantings is crucial to both the survival of the foundation species and the diverse communities they support. These findings illustrate why it is so important for restoration biologists to maintain high genetic diversity in plantings, not only to support evolutionary potential in the trees, but also to support a diverse community of organisms. Experimental field trials (common gardens) represent a robust tool that allows researchers to quantify these relationships and develop a truly "adaptive management" strategy that is based on both ecological and evolutionary principles.

Summary

Despite their intuitive appeal, ecological restoration policies encouraging the use of locally derived stock may be misguided in the face of climate change, invasive species, altered flood regimes, fire, and other biotic and abiotic challenges. Rapidly changing environmental conditions are likely to favor plant traits that are distinct from the historical conditions in which local species have evolved. Failure to recognize these crucial environmental differences can lead to long-term failure of restoration projects. While the focus of this chapter has been on riparian restoration, global change is a universal challenge and the same principles presented here apply to all ecosystems facing similar challenges worldwide.

We propose the following stepwise restoration approach to mitigate the impacts of global change:

(1) Focus first on regions that are recognized as undergoing rapid environmental changes such as riparian habitats in the American Southwest.

(2) Identify the foundation plant species that are recognized as the drivers of their respective ecosystems (e.g., cottonwoods, willows, and other dominant plants on the landscape). This is relatively easy to do as there is a wealth of published data and knowledge about the species that have the greatest functional roles in defining their respective ecosystems. As we continue to become more knowledgeable about these ecosystems in identifying hidden players such as endophytes, fungal mutualists, and pathogens (e.g., Bailey et al. 2005) that also play foundational roles, they can be added into more sophisticated studies.

(3) On Federal, State, and private lands where change is imminent or has already occurred, such as the Little Colorado River that is inundated by invasive tamarisk (*Tamarix* spp.) and camelthorn (*Alhagi maurorum*), field trials should be established to determine which populations and genotypes can survive in these altered environments. These plantings will be most effective if they comprise the range of genotypes present throughout the species' range, especially from hotter, drier climates that have similar hydrology, soils, and invasive species.

(4) Based on these field trials, a diverse set of adapted genotypes and source populations can be identified and propagated for use on adjacent lands that can best survive both current and future environmental conditions.

(5) Because different genotypes support different communities, individual genotypes and source populations can also be selected that support high biodiversity, community stability, and connectivity. Thus, as supporting high biodiversity (especially of sensitive and listed species) becomes increasingly important, managers can move from restoring at the level of species to restoring at the genotype level. They do this by using specific plant genotypes that are preferred by community members of special interest such as the southwestern willow flycatcher (Bangert et al. 2013). However, managers must be careful to avoid selecting only optimal genotypes for a specific purpose. As noted above, sometimes the suboptimal genotypes under one set of conditions outperform the optimal genotypes under another set of conditions.

The Southwest Experimental Garden Array funded by the National Science Foundation was specifically established to achieve these goals of incorporating genetics approaches in land management with the major vegetation types on the Federal, State, and private lands that the array encompasses. We emphasize that such genetic approaches have long been used in agricultural crops in which yield is the major desired outcome. The goals of wildland restoration generally emphasize creating native habitat to support high biodiversity are different than agricultural fields. But the genetic principles are the same, and land management can be improved using such methods. In the face of great environmental challenges, genetics-based approaches are cost effective and represent a key step forward to help mitigate the impacts of global environmental change.

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