
Mortality Gradients within and among Dominant Plant Populations as Barometers of Ecosystem Change During Extreme Drought

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Abstract: *Understanding patterns of plant population mortality during extreme weather events is important to conservation planners because the frequency of such events is expected to increase, creating the need to integrate climatic uncertainty into management. Dominant plants provide habitat and ecosystem structure, so changes in their distribution can be expected to have cascading effects on entire communities. Observing areas that respond quickly to climate fluctuations provides foresight into future ecological changes and will help prioritize conservation efforts. We investigated patterns of mortality in six dominant plant species during a drought in the southwestern United States. We quantified population mortality for each species across its regional distribution and tested hypotheses to identify ecological stress gradients for each species. Our results revealed three major patterns: (1) dominant species from diverse habitat types (i.e., riparian, chaparral, and low- to high-elevation forests) exhibited significant mortality, indicating that the effects of drought were widespread; (2) average mortality differed among dominant species (one-seed juniper [*Juniperus monosperma* (Engelm.) Sarg.] 3.3%; manzanita [*Arctostaphylos pungens* Kunth], 14.6%; quaking aspen [*Populus tremuloides* Michx.], 15.4%; ponderosa pine [*Pinus ponderosa* P. & C. Lawson], 15.9%; Fremont cottonwood [*Populus fremontii* S. Wats.], 20.7%; and pinyon pine [*Pinus edulis* Engelm.], 41.4%); (3) all dominant species showed localized patterns of very high mortality (24–100%) consistent with water stress gradients. Land managers should plan for climatic uncertainty by promoting tree recruitment in rare habitat types, alleviating unnatural levels of competition on dominant plants, and conserving sites across water stress gradients. High-stress sites, such as those we examined, have conservation value as barometers of change and because they may harbor genotypes that are adapted to climatic extremes.*

Keywords: climate change, fragmentation, rare habitat, water stress, ponderosa pine, quaking aspen, Fremont cottonwood, manzanita, pinyon pine, one-seed juniper

Gradientes de Mortalidad dentro y entre Poblaciones de Plantas Dominantes como Barómetros de Cambios en el Ecosistema durante Sequía Extrema

Resumen: *El entendimiento de los patrones de mortalidad de poblaciones de plantas durante eventos climáticos extremos es importante para los planificadores de conservación porque se espera que la frecuencia de tales eventos aumente, creando la necesidad de integrar la incertidumbre climática a la gestión. Las plantas dominantes proporcionan hábitat y estructura al ecosistema, así que se puede esperar que cambios en su distribución tengan efectos de cascada en toda la comunidad. La observación de áreas que responden*

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rápidamente a las fluctuaciones climáticas proporciona un panorama de futuros cambios ecológicos y ayudará a la definición de prioridades de esfuerzos de conservación. Investigamos los patrones de mortalidad en seis especies de plantas dominantes durante una sequía en el suroeste de Estados Unidos. Cuantificamos la mortalidad poblacional para cada especie en su área de distribución regional y probamos hipótesis para identificar los gradientes de estrés ecológico para cada especie. Nuestros resultados revelaron tres patrones mayores: (1) las especies dominantes en diversos tipos de hábitats (i.e., ribereño, chaparral y bosques de baja a alta elevación) presentaron mortalidad significativa, lo que indica que los efectos de la sequía fueron extendidos; (2) la mortalidad promedio fue diferente (*Juniperus monosperma* [Engelm.] Sarg.) 3.3%; *Arctostaphylos pungens* Kunth, 14.6%; *Populus tremuloides* Michx., 15.4%; *Pinus ponderosa* P. & C. Lawson, 15.9%; *Populus fremontii* S. Wats., 20.7%; y *Pinus edulis* Engelm., 41.4%); (3) todas las especies dominantes mostraron patrones localizados de mortalidad muy alta (24–100%) consistentes con gradientes de estrés hídrico. Los gestores de tierras deberían planificar para la incertidumbre climática mediante la promoción del reclutamiento de árboles en tipos de hábitat raros, lo que aligeraría los niveles no naturales de competencia sobre las plantas dominantes y conservaría sitios a lo largo de gradientes de estrés hídrico. Los sitios con estrés alto, como los que examinamos, tienen valor de conservación como barómetros de cambio y porque pueden albergar genotipos que están adaptados a cambios climáticos extremos.

Palabras Clave: *Arctostaphylos pungens*, cambio climático, estrés hídrico, fragmentación, hábitat raro, *Juniperus monosperma*, *Pinus edulis*, *P. ponderosa*, *Populus fremontii*, *P. tremuloides*

Introduction

Climate change is altering species distributions, thereby complicating conservation efforts. Current models predict biotic responses to climate change on a global scale and ignore the regional and short-term patterns and processes useful to conservation biologists and land managers (e.g., International Panel on Climate Change [IPCC] 2001; Thomas et al. 2004). Local and rapidly changing factors, such as extreme weather events, landscape modifications, invasive species, and changing genetic frequencies are likely to interact with long-term climate trends to cause more severe effects than any of the factors alone, but such interactions are poorly understood (Loehle & LeBlanc 1996; Gutschick & BassiRad 2003; Pounds & Puschendorf 2004). Conservation planners must understand how climate drives ecological changes at spatial and temporal scales relevant to human decision making.

The IPCC (2001) predicts an increase in extreme weather events and a 66–90% chance of increased mid-continental drought frequency; thus, more studies on the effects of climate perturbations on ecosystems are needed. As a primary objective in long-term climate change monitoring, the National Research Council (NRC 1990) called for the identification of specific sites within ecosystems to be designated as barometers of climate change. These sensitive areas will yield information about the effects of climate on all ecosystems and have high conservation value. A decade later, the National Ecological Observatory Network (NEON 2000), a large-scale environmental monitoring initiative, named ecotones and transition zones as useful barometers. According to the IPCC (2001), to assess ecosystem vulnerability and prioritize conservation efforts, in situ studies of ecosystem

change are more realistic than those that suggest species migration, but all the in situ studies cited in their report are a posteriori or paleoecological, and none document a mortality event in progress. Identification of the stress gradients affecting specific dominant plants will help locate barometer sites and enable monitoring and prediction of habitat change.

High-stress locations and ecotonal regions have been recognized only recently as a worthy investment of conservation funds (NEON 2000; Channell & Lomolino 2000; Smith et al. 2001). Environmental gradients should have the highest within-species levels of adaptive variation, and extreme environments should drive selection for novel genotypes (Smith et al. 2001; Gutschick & BassiRad 2003). Peripheral habitats are essential refuge locations for many species owing to their relative lack of anthropogenic influences (Channell & Lomolino 2000). By defining stress gradients in the context of dominant plants, we can manage habitats for dependent associated communities. It is important to understand the effects of extreme events on dominant vegetation because the death of dominant plant species will have cascading effects on other trophic levels (Whitham et al. 2003).

The southwestern United States experienced an extreme drought event in 2002 (NOAA 2003), which resulted in widespread mortality of dominant plants in multiple community types, including manzanita (*Arctostaphylos pungens* Kunth), quaking aspen (*Populus tremuloides* Michx.), ponderosa pine (*Pinus ponderosa* P. & C. Lawson), Fremont cottonwood (*Populus fremontii* S. Wats.), and pinyon pine (*Pinus edulis* Engelm.) (Allen 2004; this paper). United States Forest Service surveys show that as of 2003, 12,000 km² of pinyon and ponderosa pine have died in the Southwest (Breshares et al. 2005; Mueller et al. 2005).

Despite the overall high mortality across the region, localized levels of mortality were spatially heterogeneous, ranging from 0 to 100%. Little is known about what factors affect the probability of mortality in dominant woody plants during a severe drought (but see Allen & Breshears 1998; Fensham & Holman 1999; Suarez et al. 2004). Here we identify some of the major patterns of mortality associated with a record drought across diverse habitat types. Previously researchers have focused on a single ecosystem's response to water stress (Solomon & Kirilenko 1997; Allen & Breshears 1998; Horton et al. 2003), plant functional type (e.g., Condit et al. 1996; Sperry & Hacke 2002), or individual species or groups of related species (Fensham & Holman 1999; Suarez et al. 2004). To our knowledge, no studies have documented concurrent patterns of extreme drought mortality for the dominant plants that characterize a wide range of habitat types in a local region (riparian, semiarid, and low- to high-elevation forest).

The semiarid region surrounding Flagstaff, Arizona (U.S.A.), affords a unique opportunity to study local and regional patterns of drought mortality due to the presence of diverse vegetation types within a short geographic distance and the various stress gradients that have been documented previously as affecting plant water availability. Elevation varies from approximately 500–3400 m, creating a gradient of temperature and precipitation, and varied local topography creates water stress related to slope aspect (Ogle et al. 2000; Nevo 2001). Many edaphic stress gradients result from the varied age, composition, and texture of both igneous and sedimentary soils (Sullivan & Downum 1991; Cobb et al. 1997). Multiple species interactions leading to various stress-inducing or stress-relieving relationships act independently or in combination to affect patterns of mortality (Johnsen 1962; Bertness & Callaway 1994; Busch & Smith 1995). The severe drought event culminating in 2002 enabled investigations of plant mortality associated with each of these conditions.

We hypothesized that mortality would not be distributed randomly across the region but would be associated with specific factors linked to an increase in water stress. Because plant responses to stress are likely to be species-specific, the effects of extreme drought are likely to differ among species at either a regional level (mortality among species) or local scale (mortality gradients within a single species). We investigated three major hypotheses: (1) overall mortality during drought is greater in some dominant species than others, (2) stressors associated with mortality vary by species and locality, and (3) greater mortality is associated with more stressful environments. With an understanding of how drought mortality is manifested across the region, one can begin to predict future vegetation and community distributions at regional scales and incorporate climate change predictions into conservation efforts.

Methods

Owing to widespread tree mortality during the 2002 drought, we originally initiated several studies of the mortality of individual species. However, we saw an unprecedented opportunity to consider all of the studies simultaneously and address broader hypotheses about the effects of extreme drought on dominant plant distributions. We compiled data from the individual studies and then used a common method to compare mortality among species.

To examine local and regional patterns of drought-associated mortality, we conducted our research within an 80-km radius around Flagstaff, Arizona, between the fall of 2002 and the spring of 2004. We divided the research area into three zones across an elevational gradient and chose two dominant plants to represent each: (1) semiarid zone (500–1500 m, including riparian areas), where we measured mortality in Fremont cottonwood and manzanita, (2) midelevational woodland (1500–2300 m), where we measured mortality in one-seed juniper and pinyon pine, and (3) montane forests (2300–3000 m), where we measured mortality in quaking aspen and ponderosa pine. We sampled locations within the core ranges of these plants and avoided the elevational extremes of their distributions.

Regional Mortality

To test for differences in mortality levels among species, we counted live and dead trees at sites within the 80-km radius. A minimum of 14 sites per dominant plant were identified. We sampled one-seed juniper, pinyon pine, and ponderosa pine at forested locations within 2 km of state and interstate highways; all sites were >5 km apart. We counted quaking aspen in all stands encountered along U.S. Forest Service roads chosen for their proximity to aspen habitat. At each site, we picked two haphazard directions and sampled two straight-line transects until 100 trees of each dominant species present were encountered. Each tree or shrub along the transects was classified as living or dead, with the assumption that a lack of aboveground live biomass represented a mortality event. To count manzanita and one-seed juniper growing in areas where sensitive landscapes prevented the use of straight transects, we located preexisting trails >5 km apart and counted all trees near the trails. Owing to the rarity of Fremont cottonwood habitat in the region and limited presence of large accessible stands, we extended our searches beyond the 80-km radius to include sufficient sample sizes for this species. The 20 sites of the local Fremont cottonwood study (see below) were also used for the regional study, with 30 trees per site. We compared average mortality level per site across the six species.

To contrast mortality levels with predrought habitat abundance, we compared average percent mortality per

stand to the percentage of landscape occupied by each species. The predrought area occupied by each species was determined from a digital Arizona Gap Analysis Project Vegetation Map (Halvorson et al. 2001). We estimated occupied area within an 80-km radius around Flagstaff for all plants except Fremont cottonwood, which was studied within a 170-km radius.

Local Mortality

We compared documented factors associated with increased water stress (competition, soil age, soil type, elevation, distance to water, slope aspect) to within-site mortality levels (Table 1).

SEMIARID ZONE

To test whether Fremont cottonwoods growing in association with the invasive species tamarisk (*Tamarix* sp.) were experiencing greater mortality than trees in stands with no tamarisk, we selected five river systems. Twenty sites with varying tamarisk cover were chosen. We selected 30 Fremont cottonwoods at each site and classified each as living or dead. Tamarisk cover was estimated by measuring cover along three 50-m transects established perpendicular to the river, starting at the inner edge of

riparian vegetation. The percent cover along the three transects was then averaged to obtain a value for the site. We regressed cottonwood mortality levels by tamarisk cover.

To determine whether manzanita mortality increased as distance from an ephemeral wash increased, we sampled twelve, 75-m transects along washes, with six transects in the eastern direction and six transects in the western direction. We classified each shrub encountered along the transect as living or dead and measured its distance from the wash. We tested mortality levels of manzanita found growing <40 m from the wash with those found growing >40 m from the wash.

MIDELEVATION WOODLANDS

To test the effect of slope aspect on pinyon pine mortality, we chose plots encompassing 40 trees each on a north-facing slope and a south-facing slope with similar elevation, slope angles, and soil type. All pinyon pine trees within each plot were counted and recorded as live or dead. Mortality levels were compared between the two slopes. To determine whether soil depth had an effect on pinyon pine mortality, we chose two visually different cinder deposits, red and black. We established two

Table 1. Patterns of dominant plant mortality observed in this study and their potential mechanisms as documented in the literature.

<i>Patterns of mortality</i>	<i>Potential mechanisms</i>	<i>References</i>
Fremont cottonwood association with invasive species tamarisk	Fremont cottonwoods may depend more on surface soil moisture during water stress high salinity levels can inhibit surface soil moisture use tamarisk increase water use and growth in saline conditions, and individual plants use more water when growing in dense thickets	Reily & Johnson 1982; Vandersande et al. 2001 Busch & Smith 1995; Devitt et al. 1997; Glenn et al. 1998; Vandersande et al. 2001
Manzanita distance from water course	there may be a drop in water table at increased distance from wash	Masek Lopez & Springer 2002
One-seed juniper association with grasses	competition with understory vegetation may increase water stress	Teague et al. 2001
soil type	a stress gradient exists between coarse-cinder and finer-textured soils	Cobb et al. 1997
Pinyon pine slope aspect	more stressful conditions exist on slope aspects oriented toward the equator	Ogle et al. 2000; Nevo 2001
soil depth	deep cinders act as a mulch and retain more soil moisture than shallow cinders	Sullivan & Downum 1991
Ponderosa pine soil age	edaphic stress decreases with soil age due to higher water availability in older cinder soils	P. Selmants, personal communication;
nurse association/competition	facilitation is important when abiotic stress is high, but as abiotic stress decreases, competition becomes a larger factor in plant mortality	Bertness & Callaway 1994; Callaway et al. 2002
Quaking aspen elevation	temperature and precipitation gradients correlated with elevation cause higher stress at lower elevations a late freeze occurred in 1999 when low-elevation trees were leafing out, compounding other stressors	Allen & Breshears 1998 M. Manthei, personal communication

random 20-m² plots in both red and black cinders and measured soil depth at 25 locations within each plot. We placed plots along north- and east-facing slopes with the same elevation and slope angle to constrain these potentially confounding factors. Every pinyon pine within a plot was classified as living or dead, and pinyon mortality levels were compared between the two soils.

To investigate whether association with grasses affected mortality in one-seed juniper, we compared mortality rates of one-seed juniper growing in a grassland habitat (area visually dominated by grass cover) and an adjacent nongrassland habitat (area nearly devoid of grasses). We chose a site at the edge of a volcanic cinder field that included both grassland and nongrassland habitat. We sampled a 200-m-long, 30-m-wide belt transect across the study area. We counted 181 one-seed juniper trees along this transect and classified each tree as living or dead and as occurring in grassland or nongrassland. Mortality levels in and out of grassland were compared.

MONTANE FORESTS

To determine whether soil age and nurse-plant associations affect mortality levels of ponderosa pine seedlings, we sampled four 100-m transects at three differently aged volcanic soil sites as defined by Moore et al. (1974): 0.92 million years old, 0.33 million years old, and 0.15 million years old. We recorded all ponderosa pine seedlings within 20 m of the transects. We noted whether each seedling was growing within 3 cm of another plant or sheltering feature (nursed) or in the open (not nursed) and classified each as living or dead. We compared the mortality levels of seedlings that were nursed and those that were not at all soil ages. To determine whether soil age affected adult ponderosa pine mortality, we classified each mature ponderosa pine along each transect as living or dead and compared mortality of adult ponderosa pine among soil ages.

To determine whether quaking aspen mortality differed along an elevational gradient, we located two high (>2900 m), six intermediate- (2600–2900 m), and four low-elevation (2300–2600 m) sites. Four transects were established at each site, and 100 quaking aspens were counted and categorized as either living or dead. We correlated mortality levels of quaking aspen with elevational ranges.

Statistical Analyses

For comparisons with categorical response and independent variables, we applied the likelihood ratio χ^2 test. In one case, we had two independent variables and used a $2 \times 3 \times 2 \chi^2$ test in conjunction with post hoc Wald effect tests. Independent *t* tests were used to analyze data with binary independent variables and continuous response variables if the assumptions of normal distribution and

homoscedascity of variance were met. We tested equality of variance with Bartlett's test ($p > 0.05$) and normality of the distribution with the Shapiro-Wilk test ($p > 0.05$). When the data did not meet these criteria, we used the nonparametric Mann-Whitney *U* test. We used least squares linear regression in cases where the data consisted of a continuous response variable and continuous independent variable. To test for differences in regional mortality among dominant species, we used a Welch analysis of variance (ANOVA) because we were unable to correct the heteroscedascity of variance. A post hoc Dunnett's T3 test was used to determine which species were significantly different from one another. All statistics were performed in JMP-IN 4.0 (SAS Institute 1999), except the Dunnett's T3 test, which was completed in SPSS 11.5 (SPSS 2002).

Results

Regional Mortality

At the regional level, pinyon pine had greater mortality (41.4%/stand) than all of the other dominant species except Fremont cottonwood, and one-seed juniper had lower mortality (3.3%) than pinyon pine, ponderosa pine, and quaking aspen ($F_{5,41.524} = 12.6938$, Welch ANOVA $p < 0.0001$; Fig. 1). The mortality levels of dominant plants that characterize rare habitat types (those found in <2% of the study area) were similar, whereas the mortality of common dominants differed significantly. The

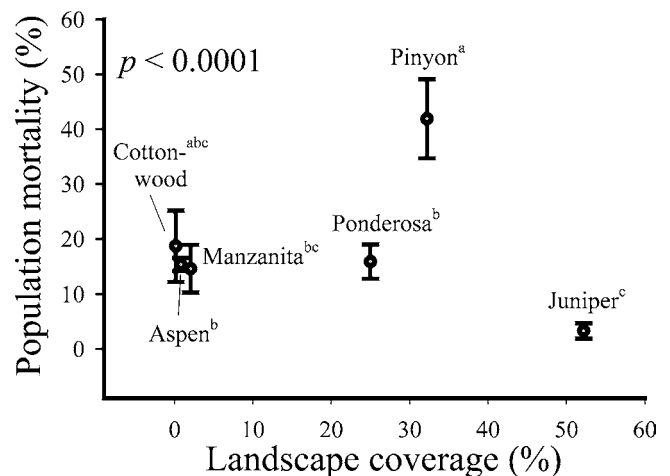


Figure 1. Among-species patterns in dominant plant mortality compared with percentage of study area dominated or codominated by study species (due to overlap, sum > 1). Shared letters indicate no significant difference detected with Dunnett's T3 (bars represent 1 SE; *p* value from Welch analysis of variance).

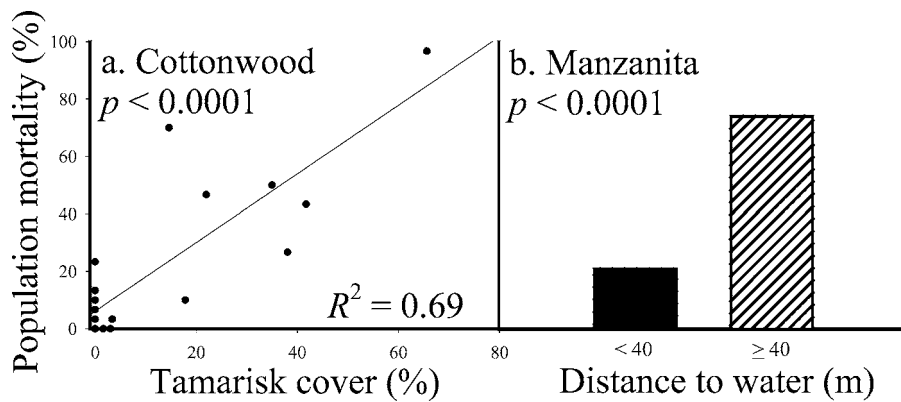


Figure 2. Local-scale dominant plant mortality in semiarid habitats (including riparian): (a) Fremont cottonwood population mortality as a function of tamarisk cover and (b) manzanita population mortality as a function of distance to ephemeral wash.

most drought-resistant tree, one-seed juniper, also had the greatest predrought distribution.

Local Mortality

Mortality per stand varied widely, especially in pinyon pine and Fremont cottonwood, demonstrating the patchiness of mortality across the region (one-seed juniper, 0–24%; manzanita, 0–46%; quaking aspen, 7–24%; ponderosa pine, 1–83%; Fremont cottonwood, 0–97%; and pinyon pine, 0–100%).

SEMIARID ZONE

Fremont cottonwood mortality was strongly positively correlated with tamarisk cover ($F = 40.7244, p < 0.0001, R^2 = 0.69$; Fig. 2a). Mortality never exceeded 23.3% in stands with <5% tamarisk cover, whereas mortality reached 97% in a stand with 66% tamarisk cover. The mortality of manzanita growing >40 m from the wash was three times greater than that of those growing near the water course ($\chi^2 = 15.215, p < 0.0001$; Fig. 2b). Plants growing within 40 m of the wash had only 16.2% mortality, whereas 52.8% of the more distant plants died.

MIDELEVATION WOODLANDS

Mortality of pinyon pines growing on a southern aspect was an order of magnitude greater than that of those growing on a northern aspect ($\chi^2 = 53.809, p < 0.0001$;

Fig. 3a). Only 9% of the trees growing on the north-facing slope died, whereas 93% of trees on the south-facing slope died.

A localized edaphic stress gradient also existed within slope aspects. Black cinders were four times deeper than red cinders ($\chi^2 = 29.018, p < 0.0001$). In black cinder soils, 15% of the trees died, whereas in adjacent red cinder soils, 81% died ($\chi^2 = 38.668, p < 0.0001$; Fig. 3b).

One-seed juniper had higher mortality when growing in association with grasses. Approximately 70% of one-seed junipers in grassland areas died, whereas only 20% of one-seed junipers growing without grasses died ($\chi^2 = 42.153, p < 0.0001$; Fig. 3c). Soil type also changed across this abrupt mortality gradient; grasses were absent in deep cinder soils and present in finer soils.

MONTANE FORESTS

The relationship between ponderosa pine seedling mortality and competition/nurse associations differed with soil age (whole model $\chi^2 = 28.6660, p < 0.0001$; Wald χ^2 for nursing = 4.0657, $p = 0.04$; for soil age = 25.5492, $p < 0.0001$; Fig. 4a). In older soils, ponderosa pine seedlings growing in close association with mature ponderosa pines or other sheltering features had nine times greater mortality than seedlings growing in the open (54% vs. 6%, respectively). In younger soils, the opposite pattern was observed, with three times less mortality in nursed seedlings (25% vs. 75%). Adult ponderosa pine mortality was significantly higher in younger soils ($\chi^2 = 105.3333, p < 0.0001$;

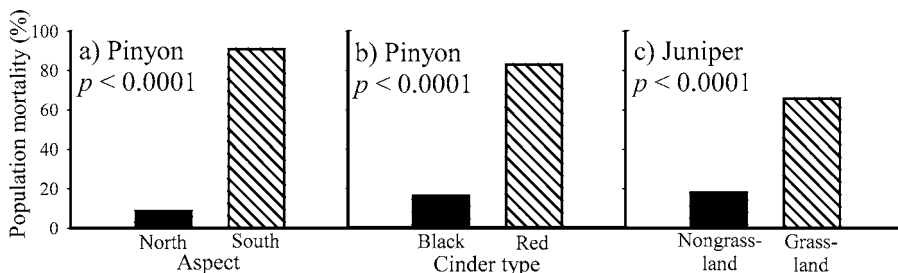


Figure 3. Local-scale dominant plant mortality in midelevation woodlands: (a) pinyon pine population mortality as a function of slope aspect, (b) pinyon pine population mortality as a function of dominant cinder type, (c) one-seed juniper population mortality as a function of landscape type (nongrassland vs. grassland).

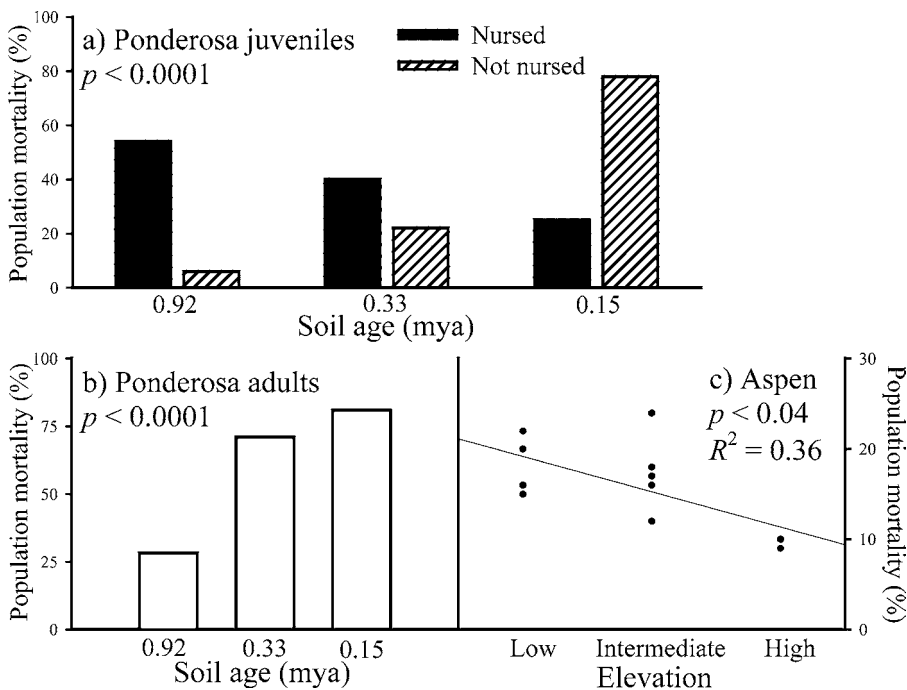


Figure 4. Local-scale dominant plant mortality in montane forests: (a) ponderosa pine juvenile mortality rate on differently aged soils (mya = time of deposition, in million years ago) as a function of nursing status and, (b) ponderosa pine adult mortality rate as a function of soil age, and (d) quaking aspen population mortality as a function of elevation.

Fig. 4b). Mortality was 81% in younger cinder soils, 70% in intermediate soils, and 29% for trees growing in the older cinder soils.

Quaking aspen mortality was negatively correlated with elevation ($F = 5.6969$, $p < 0.04$, $R^2 = 0.36$; Fig. 4c). Quaking aspen had 9.5% mortality at high-elevation sites, 16.5% mortality at sites with intermediate elevation, and 18.3% mortality at low-elevation sites.

Discussion

Anticipated Conservation Challenges

The high variation in mortality shows that mortality was patchy for all species (see also Fensham & Holman 1999; Suarez et al. 2004). Local stress gradients occurred in a matrix rather than just at the peripheries of plant distributions, driving mortality within some sites well above average regional levels. Projections of species' future distributions could be problematic if they are based on generalized "climate envelopes" confined by temperature, precipitation, and seasonality without regard for finer-scale processes (Loehle & LeBlanc 1996; IPCC 2001; Thomas et al. 2004). As the frequency of extreme drought increases, plant mortality is likely to occur in rapid pulses rather than gradual declines. This may result in isolated relict patches, which may in turn inhibit the ability of plants to recover and expand into more hospitable environments (Hewitt & Kellman 2004).

The dynamics of postdrought vegetation changes depend on the magnitude of mortality that a particular species suffers and on the relative loss of habitat based on pre- versus postdrought abundance. Some habitat-

defining species fall into an ecologically sensitive classification of low regional abundance and high mortality, which could have major biodiversity consequences. The risks to plants with the most restricted distributions include inhibited pollen flow, diminished pollinator populations, genetic bottleneck events, and greater competition from opportunistic and drought-resistant species (Young et al. 1996).

The effects of drought on dominant plants can affect thousands of associated community members across trophic levels, including mycorrhizal mutualists (e.g., Swaty et al. 2004), arthropod communities (e.g., Cobb et al. 1997; Wimp et al. 2004; Bangert et al. 2005), and vertebrates (e.g., Brown et al. 2001). Changes in genetic diversity and frequencies of specific genotypes in dominant plants can be expected to affect entire ecosystems (Whitham et al. 2003; Wimp et al. 2004; Bangert et al. 2005) and have evolutionary consequences (Nevo 2001; Grant & Grant 1993, 2002). Changes in genetic diversity may also occur in clonal species, which attain genetic diversity by passing somatic mutations to new ramets (Gill et al. 1995).

Three species in this study (Fremont cottonwood, manzanita, and quaking aspen) are capable of clonal reproduction through root sprouts, and all comprise rare habitat types. Although the loss of genetic diversity in clonal species is difficult to quantify, local analyses of aspen clones reveal genetic variation between ramets of related clones (N. Meneses, unpublished data). Sapling survival is rare in Fremont cottonwood and quaking aspen (Fleischer 1994; Bailey & Whitham 2002), so any loss of above-ground biomass can critically decrease habitat availability for dependent species.

The combined effects of this mortality event will overlap to create a very different landscape. For example, our results show that mature ponderosa pine trees are dying on younger soils where they also serve as nurse plants for ponderosa pine seedlings. Ongoing drought will likely limit the ability of ponderosa pine to regenerate in younger soils and could result in a dominance shift. Fremont cottonwoods may become locally extinct in areas where exotic tamarisk cover is high, and manzanita may become more restricted to ephemeral washes. Higher quaking aspen mortality at lower elevations may result in a shift to higher elevations on the San Francisco Peaks and other mountain ranges. Pinyon pine is being locally fragmented by stresses associated with soil depth and slope aspect. We predict that increased drought severity and frequency will lead to an expansion of one-seed juniper into areas where pinyon pine decline (Gosz 1992; Linton et al. 1998; Mueller et al. 2005).

Potential Conservation Solutions

Understanding changes in dominant plant distribution is essential to habitat preservation in a changing climate. The impact of dominant plants on large numbers of associated community members, along with the ease of delineating dominant plant distributions and their usefulness for identifying habitat types, merits their inclusion in conservation strategies. Managers must plan for climate change by preserving areas that can buffer a large range of future climate scenarios. This requires conservation of dominant plants across their entire ranges, including both high- and low-stress sites (Smith et al. 2001).

Within populations, individuals will experience different levels of drought severity according to their placement on the land, and different species within a single site will have different levels of sensitivity (Suarez et al. 2004; Gutschick & BassiRad 2003). Multiple processes associated with ecosystem degradation (fragmentation, loss of genetic diversity, habitat loss) can arise from a single event such as drought, fire, or pathogen outbreak. Conservation plans need to address the complete extent of environmental conditions and the diverse microsites that compose a species' range (Smith et al. 2001).

We believe that conservation of imperiled habitat types with high endemism (a hotspot-like approach) is essential for conserving regional biodiversity. If rare hotspot habitat types are lost, entire communities and their associated species could disappear. Fremont cottonwood, manzanita, and quaking aspen are found in <2% of our study area, and each experienced >14% mortality. It is important to understand and potentially alleviate the factors that could further these species' decline because their dependent communities are already confined to limited areas.

Locally, proactive measures aim to increase abundance of the dominant plants that comprise the rarest habitat

types, maintain water availability for dominant riparian species, and decrease unnaturally high levels of competition in forests (Grand Canyon Trust 2005). Fenced grazing exclosures encourage seedling survival for quaking aspen and Fremont cottonwood. Water rights from retired grazing leases are, in some cases, being turned over to the State Division of Wildlife Resources, and exotic species are being removed from many riparian corridors. Prescribed fires and thinning treatments alleviate competition in overcrowded ponderosa pine forests.

Efforts to preserve forest structure must also conserve evolutionary processes (Smith et al. 2001). Because geographic differentiation can lead to genetic adaptation for specific conditions, genes for stress tolerance may arise in plant populations growing in chronically stressful conditions (Morgenstern 1996). For example, results of local studies show that growing conditions for pinyon pine in the cinder fields of northern Arizona are more stressful than adjacent noncinder sites (Mopper et al. 1991; Ogle et al. 2000; Brown et al. 2001) and that sites that suffer high mortality in one drought event are also more likely to suffer high mortality in subsequent droughts (Mueller et al. 2005). Such constant abiotic stress may favor drought-adapted genotypes (Mopper et al. 1991; Cobb et al. 1997; Mitton et al. 1998) that may be best adapted to present and future environmental conditions, making them vital to the survival of the species.

Identifying Barometers of Change

According to the NRC (1990) and NEON (2000), land plots need to be designated as barometers of change in places where climatic effects on ecosystems will be apparent and where long-term monitoring and instrumentation can occur. Research aimed at predicting drought-related changes should focus on dominant plant populations subject to the greatest drought impacts. For example, our results showed that locations with poor soil quality, southern exposure, low elevations, and high levels of competition suffered mortality during a drought event. Dominant plant monitoring must occur at multiple scales to detect fragmentation processes and to be useful to conservation planners. Ecosystems at barometer sites will be the first to react to dry conditions, and ongoing monitoring will yield information about community trajectories and resilience.

Pinyon pine suffered the most mortality in 2002 and began to die off at the start of the drought in 1996 (e.g., Ogle et al. 2000), 7 years before the other less-sensitive species in our study. This indicates that pinyon pine is an especially sensitive indicator of climate change. In addition, the fact that pinyon pine is widespread (i.e., a codominant of the third largest vegetation type in the United States; West 1984) and its geographic distribution has been sensitive to climatic changes over the last 40000 years (Betancourt 1987; Betancourt et al. 1990) further supports this species as an indicator of climate change.

Conclusion

There is abundant literature predicting the effects of climate change on species' ranges, but climate change models are rarely incorporated into conservation plans. The spatial and temporal scales of climate models are disconnected from the scales of land parcels and actions that managers must work within. Our results demonstrate that extreme drought can cause sudden and dramatic changes in the abundance and spatial arrangement of dominant plants, and that site characteristics will differentially affect the dominant species that characterize many vegetation types. The key to maintaining resilient populations of dominant plants will be to conserve areas that are subject to a wide variety of environmental extremes, including sites that are under stress, while restoring habitat structure to increase rare habitat abundance and reduce water stress on dominant plant populations.

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