

# Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts

REBECCA C. MUELLER, CRESCENT M. SCUDDER, MARIANNE E. PORTER\*, R. TALBOT TROTTER III, CATHERINE A. GEHRING and THOMAS G. WHITHAM

Department of Biological Sciences and Merriam Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011-5640, USA, and \*Department of Ecology and Evolution, University of California at Irvine, Irvine, CA 92676-2525, USA

## Summary

**1** Although drought frequency and severity are predicted to increase across numerous continental interiors, the consequences of these changes for dominant plants are largely unknown. Over the last decade, the south-western US has experienced six drought years, including the extreme droughts of 1996 and 2002, which led to widespread tree mortality across northern Arizona.

**2** We examined the impact of these droughts on the co-dominant tree species of the pinyon–juniper woodland (*Pinus edulis* and *Juniperus monosperma*), a major vegetation type in the US.

**3** Pinyon mortality following both droughts was 6.5-fold higher than juniper mortality. In addition, large pinyons suffered 2–6-fold greater mortality than small pinyons, a pattern associated with higher mortality of reproductively mature trees and survival of smaller pinyons resulting from facilitation by established vegetation. Differential mortality of large pinyons resulted in a vegetation shift such that the pinyon–juniper woodlands are becoming dominated by juniper, a species that is typical of lower elevations and more arid conditions.

**4** Sites that experienced high pinyon mortality during the first drought suffered additional mortality during the second drought, so that reductions in tree densities and the resulting release from below-ground competition did not buffer surviving pinyons against additional mortality during the second drought. Such repeated mortality events also suggest that these stands may suffer chronic stress.

**5** Reductions in biotic associations (e.g. avian seed dispersers, ectomycorrhizas and nurse plants) that will probably result from extreme mortality of large pinyons ensure that the observed vegetation shifts will be persistent. Because approximately 1000 species are associated with pinyon pine, the shift in the structure of these woodlands has large-scale community consequences.

*Key-words:* climate change, differential mortality, drought, facilitation, *Juniperus monosperma*, *Pinus edulis*

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## Introduction

Recently, increased focus has been placed on the effects of global climate change on ecosystems and ecosystem processes. Projected changes include increased levels of

carbon dioxide, elevated temperatures, and increased frequency and severity of drought (IPCC 2001).

Increases in drought are of particular interest because drought has the capacity to cause extreme vegetation changes, particularly in arid and semi-arid ecosystems (Allen & Breshears 1998; Hanson & Weltzin 2000). Because these ecosystems already tolerate low baseline water levels, they may be particularly sensitive to climate

changes (Risser 1995; Hanson & Weltzin 2000), and may act as barometers of change that will occur later in other ecosystems (Brown *et al.* 2001). Reduced precipitation may cause shifts in plant composition, distribution and abundance (Stephenson 1990), and extreme or prolonged drought can result in widespread mortality of plants. For example, in New Mexico, the drought that occurred from 1953 to 1958 caused high levels of mortality of ponderosa pine, which resulted in a rapid and persistent upward shift in the pinyon–juniper/ponderosa ecotone (Allen & Breshears 1998). In addition, high levels of stress that influence plant performance can have cascading effects through many trophic levels (Kuske *et al.* 2003). Such effects were observed in Borneo, where drought-induced mortality of figs, a keystone species, resulted in severely reduced reproduction and local extinction of co-evolved pollinators, with implications for numerous other dependent organisms (Harrison 2001).

Although drought can be a potent force driving community change, relatively few studies have examined the effects of drought in natural ecosystems, and arid and semi-arid ecosystems have received less attention than more mesic ecosystems (but see Allen & Breshears 1998). Currently, the south-western US is experiencing droughts like those predicted for most mid-continental land interiors; from 1995 to 2004, the south-west experienced six drought years, including the severe droughts of 1996 and 2002 (<http://www.noaa.gov>), which resulted in widespread tree mortality. Aerial surveys of the south-western US show that as of 2003, 12 191 km<sup>2</sup> of pinyon and ponderosa pine had died (N.S. Cobb, personal communication). These major drought events make the south-west a model system for studying the effects of predicted climate changes.

We examined the impacts of the 1996 and 2002 severe droughts on patterns in mortality of pinyon pine (*Pinus edulis* Engelm.) and one-seed juniper (*Juniperus monosperma* Engelm.), co-dominant species of the pinyon–juniper woodland, the third largest vegetation type in the continental US (West 1984). We addressed four questions. First, was drought-induced mortality differential with respect to tree species (i.e. pinyon vs. juniper)? Although previous studies have shown that juniper is more drought-tolerant than pinyon (Breshears *et al.* 1997; Linton *et al.* 1998), the influence of differential species mortality in altering woodland composition has not been examined. Second, was the probability of mortality related to tree size class, and do reproductive maturity and facilitation by established vegetation contribute to the observed patterns? Variability in growth has been shown to influence pinyon mortality (Ogle *et al.* 2000), but size-related pinyon mortality has not been addressed. Third, did sites that suffered high pinyon mortality as a result of the 1996 drought experience additional mortality in 2002? Repeated tree mortality in response to successive severe droughts could suggest that these sites suffer chronic stress. Fourth, if mortality is differential with respect to tree species and size class, how extensive were the vegetation shifts that occurred, and

what are the potential implications of these shifts for the dependent communities? Differential mortality among species and size classes can lead to changes in forest composition (Slik 2004), which can in turn impact dependent communities (Kuske *et al.* 2003). An estimated 1000 species from diverse taxa are associated with pinyon (Whitham *et al.* 2003), so that increased juniper dominance may result in altered community composition within these woodlands.

## Methods

### STUDY SITES

We selected 11 sites across 85 km of the San Francisco volcanic field in northern Arizona. Sites were established in 1999 following the severe drought of 1996, and were re-surveyed after the extreme drought of 2002. Dominant overstorey vegetation at these sites was pinyon pine and one-seed juniper. Common shrub species included rabbitbrush (*Chrysothamnus nauseosus* Pall.) and Apache plume (*Fallugia paradoxa* D. Don). Sites were located in the centre of the elevational distribution of the pinyon–juniper woodland, with elevations ranging from 1975 to 2250 m a.s.l. Soils within each site were identified using classification surveys conducted by the United States Department of Agriculture Ecosystem Survey for Coconino County (USDA ESC) and included Typic Ustorthents, Typic Haplustalfs, Vitrandic Ustochrepts, Typic Haploborolls and Lithic Ustochrepts. Palmer drought severity index (PDSI) for northern Arizona (AZ Division 2) was –2.37 in 1996 and –4.36 in 2002 (negative values indicate drought conditions). Annual precipitation was 29.44 cm in 1996 and 25.53 cm in 2002 (mean annual precipitation from 1937 to 2000 was 37 cm) (<http://www.noaa.gov>).

### PINYON AND JUNIPER MORTALITY MEASUREMENTS

To quantify tree mortality in response to two successive droughts, one permanent plot designed to include 100 pinyon trees was placed within each site, and the four corners were marked with rebar. Plot size ranged from 1200 to 5000 m<sup>2</sup>. Within each plot, all trees were noted as living or dead, and the basal trunk diameter (BTD) of all pinyons and the crown width of all junipers were measured. In 1999, standing dead pinyons were classified as 1996 dead because episodic mortality was documented in 1996 (Ogle *et al.* 2000) and 1997 and 1998 were not drought years; PDSI for northern Arizona (AZ Division 2) was 0.90 in 1997 and 1.79 in 1998 (<http://www.noaa.gov>). Stand-level pinyon and juniper mortality from 1996, 2002 and the cumulative mortality from both droughts were compared using paired *t*-tests. To evaluate the mortality of different size classes of pinyons, a regression analysis comparing percentage mortality at 1.0-cm size-class intervals was performed. A second linear regression was performed

to determine if stand-level pinyon mortality in 1996 was a predictor of additional pinyon mortality in 2002. All regression analyses were performed with SigmaPlot 9.0, and all other data analyses were performed with SPSS v. 12.0.

#### POTENTIAL ASSOCIATIONS WITH PINYON MORTALITY

To address whether reproductive maturity influenced mortality, a 100 m × 10 m plot was placed at six randomly selected sites within the same geographical range as the study sites. Presence of strobili or strobili scars and BTD of all pinyons were noted. We measured strobili because maturity for male function precedes maturity for female function in pinyons. To determine if reproductive maturity and mortality were related, we performed a regression analysis comparing the percentage of reproductively mature pinyons in 1.0-cm size classes against the percentage mortality in each size class. In addition, we compared the percentage mortality of size classes in which all trees were reproductive with those in which all trees were non-reproductive using a *t*-test.

To determine if seedling associations with established vegetation were beneficial (i.e. facilitative rather than competitive), we compared the mortality of pinyon seedlings (BTB < 3.0 cm) located in vegetation inter-spaces and in the understories of trees and shrubs in all plots using a chi-squared test. Pinyon seedling mortality from the 1996 drought was measured in 1999, and mortality from the 2002 drought was measured in 2002. To determine if seedlings (living and dead) were more likely to be found in association with adult conspecifics or other vegetation, we also used a chi-squared test.

#### VEGETATION SHIFTS IN RESPONSE TO TREE MORTALITY

To create a visual representation of the vegetation shifts resulting from differential mortality of species and pinyon size classes, we mapped all pinyon and juniper stems within a 50 m × 100 m plot at one of the 11 sites using a GPS receiver with differential correction. In addition, we measured the height, crown width and BTB of all mapped trees. Trees were placed into seedling (< 3.0 cm), juvenile (3.0 cm to > 12.0 cm) and mature (> 12.0 cm) BTB classes based on data of reproductive maturity and size class above. These data were then combined with map information within ArcGIS v. 9 to generate maps for community composition prior to 1996 and after the droughts of 1996 and 2002.

In order to quantify vegetation shifts in response to tree mortality, we compared pinyon size and pinyon vs. juniper basal area of these sites before and after the droughts. To examine if differential mortality resulted in a shift in the mean size of pinyons, we compared the mean BTB of pinyons before and after the droughts using a paired *t*-test. In addition, we compared the percentage of reproductively mature trees of all sites before and

after the droughts using a paired *t*-test. To compare basal area of pinyon and juniper, juniper BTB was computed using a regression equation correlating crown width (0.5-m size classes) to BTB ( $y = 4.1 + 12.1x$ ,  $r^2 = 0.91$ ,  $F = 129$ ,  $P < 0.001$ ). This equation was developed using independent data collected from measurements of both parameters on over 700 junipers (N.S. Cobb, unpublished data), a larger data set with improved accuracy relative to our survey work. Basal area (cm<sup>2</sup> ha<sup>-1</sup>) of pinyon and juniper at all study sites prior to the drought of 1996 and after the 1996 and 2002 droughts were compared using a paired *t*-test.

To quantify the potential impact of tree mortality on stand-level cone inputs, we measured cone production at all sites in August and September 1999, a mast year for pinyons. Within the 11 plots, all cones were counted on 20–30 trees with BTBs that ranged from 15 to 30 cm. A regression equation comparing average cone production at 1.0-cm BTB size class was computed ( $y = -79.8 + 6.61x$ ,  $r^2 = 0.80$ ,  $F = 56.1$ ,  $P < 0.001$ ) and used to estimate cone production of surviving pinyons for pre- and post-mortality years. Estimated stand-level cone production before and after the 1996 drought and after the 2002 drought was compared using a one-way ANOVA.

### Results

#### DIFFERENTIAL PINYON MORTALITY

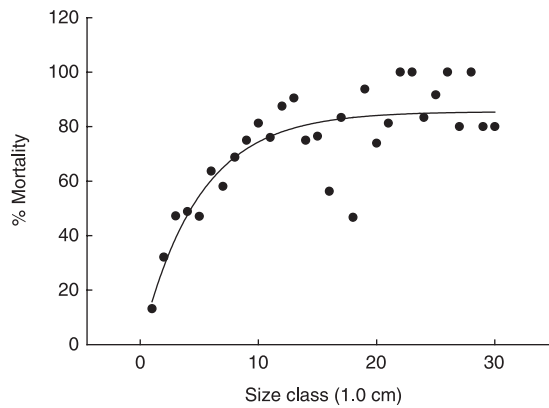
Pinyon mortality greatly exceeded juniper mortality during the droughts of 1996 ( $t = 2.86$ ,  $P = 0.008$ ) and 2002 ( $t = 5.83$ ,  $P < 0.001$ ). Pinyon mortality was  $25.9 \pm 7.03\%$  in 1996 and  $31.7 \pm 5.44\%$  in 2002, whereas juniper mortality was  $3.0 \pm 1.30\%$  in 1996 and  $4.5 \pm 3.06\%$  in 2002. Cumulative pinyon mortality was  $46.8 \pm 8.15\%$  whereas cumulative juniper mortality was only  $7.2 \pm 3.37\%$  ( $t = 4.40$ ,  $P < 0.001$ ).

Mortality of pinyons during both droughts was differential with respect to tree size. We found a positive curvilinear relationship between cumulative percentage mortality and tree BTB ( $r^2 = 0.679$ ,  $F = 69.4$ ,  $P < 0.001$ ) (Fig. 1), which demonstrates that larger trees were far more likely to die than smaller trees as a result of these drought events. Owing to the low levels of mortality observed for juniper, similar comparisons were not made for this species.

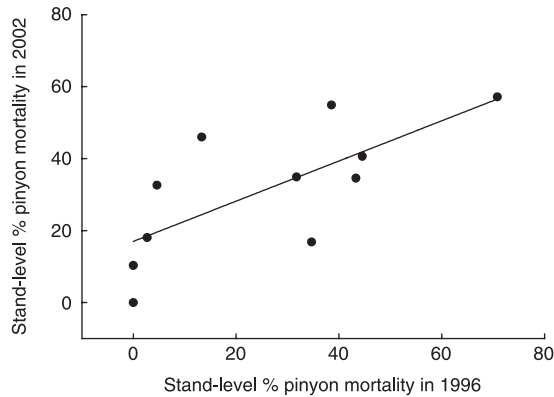
Pinyon–juniper stands that suffered high pinyon mortality in 1996 also suffered the highest mortality in 2002. Stand-level pinyon mortality resulting from the 1996 drought was positively correlated with additional pinyon mortality observed in 2002 ( $r^2 = 0.504$ ,  $F = 9.15$ ,  $P = 0.01$ ) (Fig. 2).

#### ASSOCIATIONS WITH PINYON MORTALITY

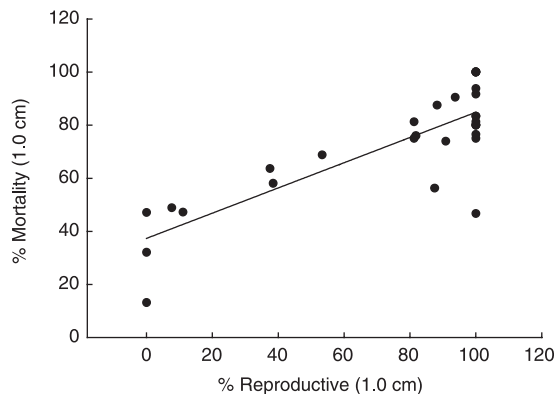
Percentage pinyon mortality was correlated with the percentage of reproductive trees in that size class ( $r^2 = 0.668$ ,  $F = 56.31$ ,  $P < 0.001$ ) (Fig. 3). Mean mortality



**Fig. 1** Percentage mortality was positively related to pinyon size class. Larger size classes of trees suffered 2–6-fold higher levels of mortality than smaller size classes.

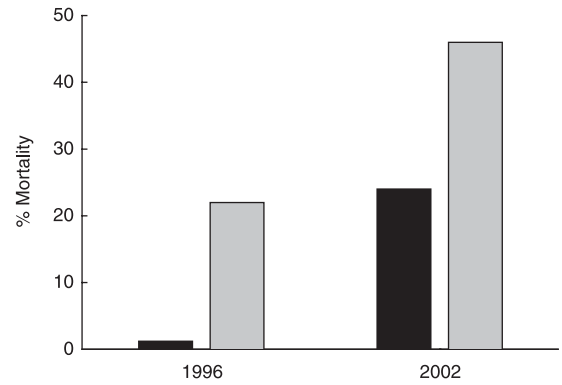


**Fig. 2** Pinyon mortality resulting from the 2002 drought was positively correlated with pinyon mortality from the 1996 drought. Sites with the highest levels of mortality in 1996 also experienced extreme pinyon mortality in 2002.



**Fig. 3** Percentage mortality of pinyons in 1.0-cm BTD size classes was significantly correlated with the percentage of pinyons that were reproductively mature for male function in the same size classes.

of size classes that were 100% reproductive was  $57.5 \pm 5.3$  cm, whereas the mean mortality of non-reproductive size classes was only  $18.2 \pm 2.4$  cm ( $t = 6.73$ ,  $P < 0.001$ ). The size at which 90% of trees were reproductively mature was 12.0 cm BTD.



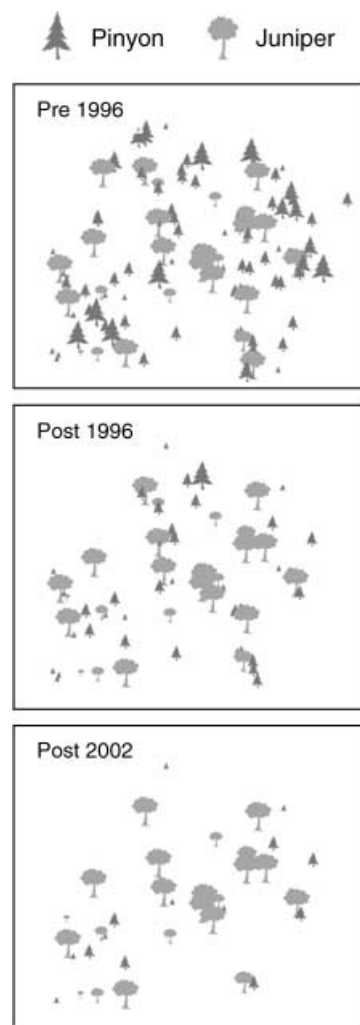
**Fig. 4** Association with established vegetation reduced mortality of pinyon seedlings 10-fold in 1996 and 2-fold in 2002, suggesting that facilitation is important for survival of seedlings during severe drought. Bars represent the percentage mortality of understorey (black bars) and open (grey bars) pinyon seedlings in all plots during 1996 and 2002.

Association with established vegetation was linked to lower mortality of small pinyons. Mortality of seedlings located in vegetation interspaces was nearly 10-fold higher during 1996, and more than two-fold higher after both droughts than seedlings in vegetation understoreys (Fig. 4). In addition, 59% of seedlings were found in association with conspecifics, compared with only 17% with junipers or shrubs and 24% in vegetation interspaces ( $\chi^2 = 13.8$ ,  $P < 0.005$ ).

#### SHIFTS IN WOODLAND STAND COMPOSITION AND STRUCTURE

Pinyon mortality was concentrated in large size classes, altering the composition of these woodlands (Fig. 5). Differential mortality resulted in a shift in the pinyon size distribution at these sites. Prior to both droughts, mean BTD was  $12.15 \pm 1.31$  cm, and after the droughts, mean BTD shifted to  $10.14 \pm 1.30$  cm ( $t = 2.18$ ,  $P = 0.03$ ). Based on the average ring width of pinyons calculated by Trotter *et al.* (2002), 2 cm BTD is equivalent to approximately 22–34 years of growth. However, a caveat regarding this estimate is that the ring width measures upon which they are based were performed on juvenile trees, and ring width probably changes as the girth of the tree increases with age (Ruel & Whitham 2002). In addition, based on the size of pinyons at reproductive maturity (12 cm), the percentage of reproductive trees in these sites shifted from 39.8% to 31.5% ( $t = 2.65$ ,  $P = 0.01$ ). Species- and size-dependent mortality is also reflected in a pronounced decline in pinyon mean basal area; prior to 1996, pinyon and juniper mean basal area ( $\text{m}^2 \text{ha}^{-1}$ ) were not significantly different, but in 2002, the mean basal area of surviving pinyons was 75% lower than the mean basal area of surviving juniper (Fig. 6a).

In addition to shifts in species dominance, estimated cone production (number of cones per stand) was reduced by the loss of whole tree inputs due to mortality of adult trees. Across all sites, estimated stand-level mast-year



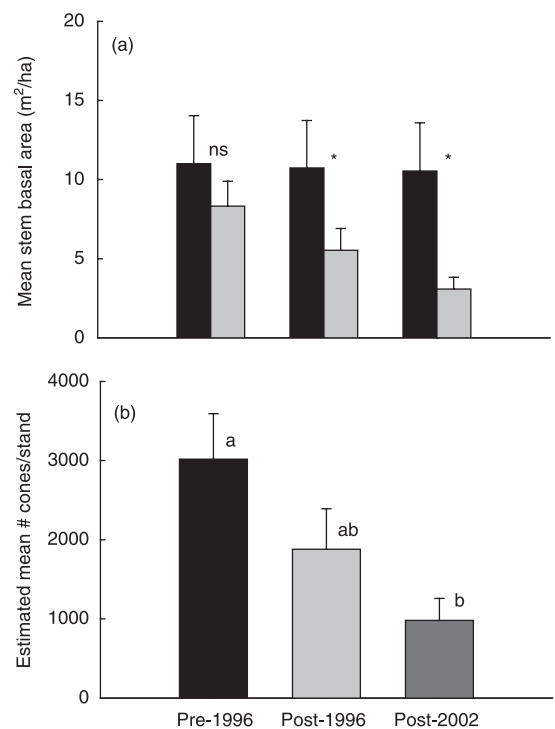
**Fig. 5** Mortality of large pinyon resulted in vegetation shifts, such that sites became dominated by juniper and smaller pinyons. Each box represents the vegetation composition of the same 50 m × 50 m plot before the 1996 drought, following the 1996 drought and following the 2002 drought.

cone production based on BTD was reduced by 67% ( $F = 4.67$ ,  $P = 0.02$ ) (Fig. 6b). Prior to 1996, estimated stand-level cone production was  $3017 \pm 576$ ; following the droughts of 1996 and 2002, estimated cone production of these sites was only  $1880 \pm 511$  and  $980 \pm 279$ , respectively.

## Discussion

### DIFFERENTIAL SPECIES MORTALITY

Juniper mortality was lower than pinyon mortality during both droughts. This result is not surprising given that members of the family Pinaceae, and particularly trees in the genus *Pinus*, are more vulnerable to drought-induced mortality than other conifers (Martinez-Vilalta *et al.* 2004). Comparative studies of pinyon and juniper have shown that juniper is able to withstand more negative leaf water potentials prior to catastrophic xylem cavitation than pinyon (Linton *et al.* 1998) and is able to utilize



**Fig. 6** Differential mortality of large size classes of pinyons resulted in changes in vegetation composition and reductions in reproductive inputs. (a) Drought-induced mortality resulted in increased dominance of juniper. Basal area of juniper (grey bars) and pinyon (black bars) were not different prior to 1996, but juniper basal area was significantly greater than pinyon basal area following the drought of 1996 and the drought of 2002. Asterisks represent significant differences at  $\alpha = 0.05$ , and ns represents non-significant differences. (b) Estimated cone inputs based on the BTD of surviving pinyons within all sites were reduced by 67% due to adult pinyon mortality resulting from the droughts of 1996 and 2002. Different letters represent significant differences at  $\alpha = 0.05$ .

intercanopy soil moisture to a greater extent than pinyon (Breshears *et al.* 1997). Juniper has also been shown to impact pinyon performance negatively. Below-ground competition with juniper resulted in reduced pinyon root biomass and ectomycorrhizal colonization (Haskins & Gehring 2004; McHugh 2004), which may contribute to increased pinyon mortality (McHugh 2004).

### FACILITATION AND PINYON SEEDLING SURVIVAL

We found that pinyon seedlings exhibited the lowest levels of mortality during severe drought, while mature tree mortality exceeded 50%. This dichotomy is probably due both to factors that promote the survival of younger trees and to factors that contribute to the mortality of older trees. Higher survival of seedlings during drought is unexpected, because the probability of tree mortality generally decreases with increasing tree size as a result of the greater capacity for nutrient acquisition and competitive ability of larger trees (Moore *et al.* 2004). This increased susceptibility is reflected in most studies

of age/size-related mortality in woody and herbaceous species, which often follow an 'L' pattern (e.g. Lawson *et al.* 1999; Chidumayo 2003).

Because of the lower mortality of juvenile pinyons beneath vegetation canopies than in the open, we suggest that nurse plant association (facilitation) is a key factor contributing to the survival of small pinyons during severe drought. The understorey microclimate often has improved nutrient and soil properties, higher soil moisture, and lower temperatures and light levels compared with interspaces (Callaway 1995, and references therein). Facilitation has been shown to increase pinyon seedling survival under harsh conditions (Callaway *et al.* 1996; Chambers 2001; Stulz 2004), although growth may be reduced due to light limitation (Callaway *et al.* 1996). Because the importance of facilitative interactions is generally greater under conditions of high abiotic stress (Bertness & Callaway 1994; Callaway *et al.* 2002), facilitation may be a mechanism by which smaller pinyons can survive periods of extreme drought in semi-arid woodlands.

#### DIFFERENTIAL MORTALITY OF LARGE PINYONS

The size-related patterns of mortality we observed were also probably due to greater vulnerability to drought stress in larger trees. Although several mechanisms could explain this pattern, we suggest that reproductive maturity and higher vulnerability to xylem cavitation of large trees are the most likely causes. Increased carbon costs associated with reproduction could contribute to higher levels of mortality for large trees. The cost of reproduction in plants is often manifested in other life-history traits, including growth and mortality (Obeso 2002), and the cost of reproduction is likely to be manifested under conditions of stress (Reznick 1985). We found a positive relationship between reproductive maturity and percentage mortality of pinyon (Fig. 3). Although these data are not conclusive, they suggest that reproductive maturity contributes to pinyon mortality during severe drought, and provide an explanation for the increase in mortality up to BTD ~12.0 cm (Fig. 1).

Another potential mechanism for higher levels of mortality of larger pinyon size classes is higher susceptibility of large trees to catastrophic xylem cavitation. Although large trees have a higher capacity for nutrient capture and water storage than small trees, large trees may be more susceptible to mortality during prolonged periods of drought (Slik 2004) because larger trees have higher water use per unit time than smaller trees (Meizner 2003). For example, higher mortality of large eucalypts during drought was attributed to the greater resistance to xylem cavitation of smaller trees (Rice *et al.* 2004), and Slik (2004) found similar patterns of drought-related mortality in several species of rainforest trees. Although these findings demonstrate that larger trees suffer higher mortality during severe drought, neither study included the smallest size classes of trees,

so the relative susceptibility of seedlings to drought is unknown for these systems. Although, to our knowledge, comparative studies on xylem cavitation of juvenile vs. mature pinyons have not been undertaken, Domec *et al.* (2004) found that roots of young ponderosa pine were more susceptible to catastrophic cavitation than roots of old or intermediate aged trees, suggesting that pines may exhibit different age-related susceptibility to cavitation from the tree species in the above studies.

Although outbreaks of insect herbivores, particularly bark beetles, would be predicted to result in higher mortality of mature pinyons (M.J. Santos and T.G. Whitham, unpublished data), while bark beetle populations in northern Arizona pine forests reached epidemic levels in 2002, no outbreak was recorded for 1996 (USDA 2002). Because 1996 stand-level mortality of pinyons was as high as 70%, and a similar positive relationship between size class and percentage mortality was observed in the absence of bark beetles ( $r^2 = 0.74$ ,  $F = 33.2$ ,  $P < 0.001$ ), we consider water stress to be the ultimate driving force behind these patterns of pinyon mortality.

#### CHRONIC STRESS AND PINYON MORTALITY

We found that sites that experienced high pinyon mortality in 1996 also suffered the highest levels of mortality during the 2002 drought. These repeated mortality events show that reductions in the density of trees did not buffer sites against additional mortality during a subsequent drought, so that the 'release effect' of tree mortality did not increase the ability of the survivors to endure the next severe drought (e.g. Martinez-Vilalta *et al.* 2002). Although below-ground competition with juniper has been shown to impact pinyons negatively (Haskins & Gehring 2004; McHugh 2004), our data suggest that below-ground intraspecific competition is not a major factor driving patterns of drought-induced pinyon mortality.

High mortality even following the removal of potential competitors is consistent with the hypothesis that trees exposed to chronic stresses are more susceptible to short-term stresses, such as severe drought (Pedersen 1998). In support of this hypothesis, Swaty *et al.* (2004) showed that the long-term radial growth of pinyons growing in sites of high pinyon mortality (> 30%) was significantly lower than that of pinyons growing in adjacent sites of low mortality (< 5%). Pinyons in high-mortality sites also had higher levels of water stress (Swaty *et al.* 2004), and 30% lower mast-year cone production (R.C. Mueller, unpublished data), indicating that these trees experienced chronic stress. Although no differences in abiotic factors were found to explain these differences (Swaty *et al.* 2004), Trotter (2004) showed that, across an 820-km<sup>2</sup> area of northern Arizona, pinyon mortality following the 1996 drought was significantly related to elevation, slope and aspect. The potential contributions of chronic stress to patterns of tree death are important because high mortality at the same sites

represents repeated selection events that could result in local adaptation (Nevo 2001; Grant & Grant 2002; but see Gutschick & BassiriRad 2003).

#### PREDICTED CONSEQUENCES OF DIFFERENTIAL MORTALITY

Mortality within the pinyon–juniper woodland was concentrated in larger pinyons, resulting in increased juniper dominance and a shift in the age structure of the remaining pinyon pines. Because pinyons are slow-growing, long-lived species, these vegetation shifts are likely to be long-term, and changes in stand dynamics may prevent or delay a return to pre-drought stand conditions. In addition, changes in stand dynamics and feedbacks such as the maintenance of ectomycorrhizal mutualists, available nurse plants and seed-dispersing birds may prevent or slow recruitment, further delaying a return to pre-drought stand conditions.

Reductions in the numbers of avian seed dispersers active in the pinyon–juniper woodland are probably associated with the loss of mature pinyons. In the pinyon–juniper woodland, bird dispersers abandoned individual pinyons and stands when cone crops were reduced by 57% due to chronic insect herbivory (Christensen *et al.* 1991). Predicted cone crop losses in our study sites were similar in magnitude, with stand-level reductions averaging 67% (Fig. 6b). If avian response to cone crop reduction resulting from pinyon mortality is similar to insect-induced crop losses, abandonment of sites by bird dispersers is likely. Because pinyons are co-evolved with their corvid seed dispersers (VanderWall & Balda 1977) and pinyon seeds require burial by birds or mammals in order successfully to germinate and establish (Chambers 2001), the loss of avian dispersers will probably negatively impact pinyon recruitment.

Pinyons also require ectomycorrhizal mutualisms for successful establishment (Gehring & Whitham 1994). In many pinyon–juniper woodlands, pinyons are the only known hosts of ectomycorrhizal fungi, while juniper and shrubs support arbuscular mycorrhizas (Haskins & Gehring 2005). As a result, reduced fungal inoculum resulting from low pinyon densities will probably limit the recruitment of seedlings in these altered systems. This hypothesis is supported by two data sets. First, juniper-dominated sites have reduced levels of soil ectomycorrhizal fungal inoculum relative to co-dominant and pinyon-dominated sites (Haskins & Gehring 2005). Second, Swaty *et al.* (2004) found that mature pinyons in high-mortality sites supported 50% lower levels of ectomycorrhizal colonization and fungal species richness than adjacent low-mortality sites.

In addition to ectomycorrhizas, pinyons also require nurse plants to establish in harsh environments (Chambers 2001). The positive vs. negative impacts of dead nurses on understory seedlings has not been demonstrated for pinyons, but eventual treefall in areas of high pinyon mortality could render the dead pinyons inadequate for pinyon seedling facilitation in the long term, because

pinyons establish with woody debris only occasionally (Chambers 2001). As a result of decreased conspecific nurse plant availability, pinyon recruitment will occur primarily in association with junipers or shrubs. Although the relative benefits of these different types of nurses are unknown, the spatial segregation with conspecific nurses and high mortality of juvenile pinyons in open spaces that we observed in this study suggest that pinyons may be important for pinyon establishment in these sites. However, although nurse plant mortality will probably negatively impact pinyon recruitment, the death of the overstorey plant may result in above- and below-ground competitive release for juvenile trees that established prior to these droughts (e.g. Anderson *et al.* 2001).

#### COMMUNITY IMPLICATIONS OF SEVERE DROUGHT

In the pinyon–juniper woodland, drought-induced mortality of pinyon will impact a diverse dependent community, from microbes to vertebrates (Schowalter *et al.* 1999; Brown *et al.* 2001; Kuske *et al.* 2003; Whitham *et al.* 2003). Because approximately 1000 species are associated with pinyon pine, the shift in vegetation composition toward higher juniper dominance must be associated with restructuring of these dependent communities (Whitham *et al.* 2003). Extreme pinyon mortality reduces available habitat for species that depend on pinyon for survival, leading to altered community structure of species such as ectomycorrhizal fungi (Swaty *et al.* 2004). Furthermore, the death of mature plants reduces or eliminates organisms, including seed-dispersing birds (Christensen *et al.* 1991), insects (Ruel & Whitham 2002) and microbial decomposers (Kuske *et al.* 2003) that are restricted to mature trees, leaving only those species that can utilize juvenile trees.

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#### References

- Allen, C.A. & Breshears, D.D. (1998) Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Science USA*, **95**, 14839–14842.
- Anderson, L.J., Brumbaugh, M.S. & Jackson, R.B. (2001) Water and tree–understory interactions: a natural experiment in a savannah with oak wilt. *Ecology*, **82**, 33–49.
- Bertness, M.D. & Callaway, R.M. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.

- Breshears, D.D., Myers, O.B., Johnson, S.R., Meyer, C.N. & Martens, S.N. (1997) Differential use of spatially heterogeneous soil moisture by two semiarid species: *Pinus edulis* and *Juniperus monosperma*. *Journal of Ecology*, **85**, 289–299.
- Brown, J.H., Whitham, T.G., Morgan Ernest, S.K. & Gehring, C.A. (2001) Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science*, **293**, 643–650.
- Callaway, R.M. (1995) Positive interactions among plants. *Botanical Review*, **61**, 306–349.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D. & Cook, B.J. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.
- Callaway, R.M., DeLucia, E.H., Moore, D., Nowak, R. & Schlesinger, W.H. (1996) Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. *Ecology*, **77**, 2130–2141.
- Chambers, J.C. (2001) *Pinus monophylla* establishment in an expanding pinon–juniper woodland: environmental conditions, facilitation and interacting factors. *Journal of Vegetation Science*, **12**, 27–40.
- Chidumayo, E.N. (2003) Population ecology of an afro-tropical savanna herb, *Lapeirousa rivularis*, in Zambia. *Plant Ecology*, **165**, 275–286.
- Christensen, K.M., Whitham, T.G. & Balda, R.P. (1991) Discrimination among pinyon pine trees by Clark's nutcrackers: effects of cone crop size and cone characters. *Oecologia*, **86**, 402–407.
- Domec, J.-C., Warren, J.M., Meizner, F.C., Brooks, J.R. & Coulombe, R. (2004) Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia*, **141**, 7–16.
- Gehring, C.A. & Whitham, T.G. (1994) Comparisons of ectomycorrhizae on pinyon pine (*Pinus edulis*: Pinaceae) across extremes of soil type and herbivory. *American Journal of Botany*, **81**, 1509–1516.
- Grant, P.R. & Grant, B.R. (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science*, **296**, 707–711.
- Gutschick, V.P. & BassiriRad, H. (2003) Extreme events as shaping physiology, ecology and evolution of plants: toward a unified definition and evaluation of their consequences. *New Phytologist*, **160**, 21–42.
- Hanson, P.J. & Weltzin, J.F. (2000) Drought disturbance from climate change: response of United States forests. *Science of the Total Environment*, **262**, 205–220.
- Harrison, R.D. (2001) Drought and the consequences of El Niño in Borneo: a case study of figs. *Population Ecology*, **43**, 63–75.
- Haskins, K.E. & Gehring, C.A. (2004) Interactions with juniper alter pinyon pine ectomycorrhizal fungal communities. *Ecology*, **85**, 2687–2692.
- Haskins, K.E., Gehring, C.A. (2005) Evidence for mutualist limitation: the impacts of conspecific density on the mycorrhizal inoculum potential of woodland soils. *Oecologia*, doi: 10.1007/s00442-005-0115-3.
- IPCC (Intergovernmental Panel on Climate Change). (2001) *Climate Change 2001: the Scientific Basis*. Cambridge University Press, Cambridge.
- Kuske, C.R., Busch, J.D., Ticknor, L.O., Gehring, C.A. & Whitham, T.G. (2003) The pinyon rhizosphere, plant stress, and herbivory affect the abundance of microbial decomposers in soils. *Microbial Ecology*, **45**, 340–352.
- Lawson, D., Inouye, R.S., Huntly, N. & Carson, W.P. (1999) Patterns of woody plant abundance, recruitment, mortality, and growth in a 65 year chronosequence of old-fields. *Plant Ecology*, **145**, 267–279.
- Linton, M.S., Sperry, J.S. & Williams, D.G. (1998) Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. *Functional Ecology*, **12**, 906–911.
- Martinez-Vilalta, J., Pinol, J. & Beven, K. (2002) A hydraulic model to predict drought-induced mortality in woody plants: an application to climate change in the Mediterranean. *Ecological Modelling*, **155**, 127–147.
- Martinez-Vilalta, J., Sala, A. & Pinol, J. (2004) The hydraulic architecture of Pinaceae – A review. *Plant Ecology*, **171**, 3–13.
- McHugh, T.A. (2004) Belowground competition reduces root biomass and ectomycorrhizae, contributing to pinyon mortality. Masters thesis, Northern Arizona University.
- Meizner, F.C. (2003) Functional convergence of plant responses to the environment. *Oecologia*, **134**, 1–11.
- Moore, J.A., Hamilton, D.A., Jr., Xiao, Y. & Byrne, J. (2004) Bedrock type significantly affects individual tree mortality for various conifers in the inland Northwest, USA. *Canadian Journal of Forest Research*, **34**, 31–42.
- Nevo, E. (2001) Evolution of genome–phenome diversity under environmental stress. *Proceedings of the National Academy of Science, USA*, **98**, 6233–6240.
- NOAA. (2002) Climate division drought data. <http://www.ncdc.noaa.gov>.
- Obeso, J.R. (2002) The costs of reproduction in plants. *New Phytologist*, **155**, 321–348.
- Ogle, K., Whitham, T.G. & Cobb, N.S. (2000) Tree-ring variation in pinyon predicts the likelihood of death following severe drought. *Ecology*, **81**, 3237–3243.
- Pedersen, B.S. (1998) Modeling tree mortality in response to short- and long-term environmental stresses. *Ecological Modelling*, **105**, 347–351.
- Reznick, D. (1985) Cost of reproduction: an evaluation of the empirical evidence. *Oikos*, **44**, 257–267.
- Rice, K.J., Matzner, S.L., Byer, W. & Brown, J.R. (2004) Patterns of tree dieback in Queensland, Australia: the importance of drought stress and the role of resistance to cavitation. *Oecologia*, **139**, 190–198.
- Risser, P.G. (1995) The status of the science of examining ecotones. *Bioscience*, **45**, 318–325.
- Ruel, J. & Whitham, T.G. (2002) Fast-growing juvenile pinyons suffer greater herbivory when mature. *Ecology*, **83**, 2691–2699.
- Schowalter, T.D., Lightfoot, D.C. & Whitford, W.G. (1999) Diversity of arthropod responses to host-plant water stress in a desert ecosystem in southern New Mexico. *American Midland Naturalist*, **142**, 281–290.
- Slik, J.W. (2004) El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. *Oecologia*, **141**, 114–120.
- Stephenson, N.L. (1990) *Climatic control of vegetation distribution: the role of water balance*. *American Naturalist*, **135**, 649–670.
- Stulz, C.M. (2004) Conditional plant interactions: switches from facilitation to competition with decreasing environmental stress. Masters thesis, Northern Arizona University.
- Swaty, R.L., Deckert, R.J., Whitham, T.G. & Gehring, C.A. (2004) Ectomycorrhizal abundance and community composition shifts with drought: predictions from tree rings. *Ecology*, **85**, 1072–1084.
- Trotter, R.T. III (2004) *Linking climate change and community dynamics: pinyon pine stability and sensitivity in a heterogeneous landscape*. PhD dissertation, Northern Arizona University.
- Trotter, R.T., III, Cobb, N.S. & Whitham, T.G. (2002) Herbivory, plant resistance, and climate in the tree ring record: Interactions distort climatic reconstructions. *Proceedings of the National Academy of Science, USA*, **99**, 10197–10202.
- USDA Forest Service. (2002) *Forest Insect and Disease Conditions in the Southwest Region, 2002*. Forestry and Forest Health R3–03–01.



- VanderWall, S.P. & Balda, R.P. (1977) Coadaptations of Clark's nutcrackers and pinyon pine for efficient seed harvest and dispersal. *Ecological Monographs*, **47**, 89–110.
- West, N.E. (1984) Successional patterns and productivity potentials of pinyon-juniper ecosystems. *Developing Strategies for Range Management: A Report*, pp. 1301–1332. Westview Press, Boulder, CO.
- Whitham, T.G., Young, M.P., Martinsen, G.D., Gehring, C.A.,

Schweitzer, J.A., Wimp, G.M., Fischer, D.G., Bailey, J.K. & Lindroth, R.L. (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology*, **84**, 1171–1178.

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