Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon–juniper woodlands

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Abstract. Extreme drought conditions accompanied by rising temperatures have characterized the American Southwest during the past decade, causing widespread tree mortality in piñon–juniper woodlands. Piñon pine (*Pinus edulis* Engelm.) mortality is linked primarily to outbreaks of the pinyon ips (*Ips confusus* (Leconte)) precipitated by drought conditions. Although we searched extensively, no biotic agent was identified as responsible for death in *Juniperus* L. spp. in this study; hence this mortality was due to direct drought stress. Here we examine the relationship between tree abundance and patterns of mortality in three size classes (seedling/sapling, pre-reproductive, reproductive) during the recent extended drought in three regions: southwest Colorado, northern New Mexico, and northern Arizona. Piñon mortality varied from 32% to 65%, and juniper mortality from 3% to 10% across the three sites. In all sites, the greatest piñon mortality was in the larger, presumably older, trees. Using logistic regression models, we examined the influence of tree density and basal area on bark beetle infestations (piñon) and direct drought impacts (juniper). In contrast to research carried out early in the drought cycle by other researchers in Arizona, we did not find evidence for greater mortality of piñon and juniper trees in increasingly high density or basal area conditions. We conclude that the severity of this regional drought has masked density-dependent patterns visible in less severe drought conditions. With climate projections for the American Southwest suggesting increases in aridity and rising temperatures, it is critical that we expand our understanding of stress responses expected in widespread piñon–juniper woodlands.

Key words: bark beetles; density-dependent mortality; drought stress; Ips confusus; Juniperus monosperma; Juniperus osteosperma; *piñon–juniper woodlands;* Pinus edulis; *pinyon ips; Southwest USA.*

INTRODUCTION

Piñon–juniper woodlands are the third largest vegetation type in the West, covering nearly 30×10^6 ha between 1650 and 2400 m elevation (West 1999) and are vitally important for biodiversity, aesthetics, and commodity production (Mitchell and Roberts 1999). Extreme drought conditions have characterized the American Southwest during the past decade causing widespread mortality in piñon–juniper woodlands. While comparably low precipitation levels have occurred at other times in the past century, rising temperatures have accompanied the latest drought, increasing water stress on vegetation and triggering increases in bark beetle-caused mortality (Breshears et al. 2005). Drought-related outbreaks in pinyon ips (*Ips confusus* (Leconte)), have killed piñon pines over 12 000 km² in the Southwest (Breshears et al. 2005, Shaw et al. 2005). Cumulative five-year mortality rates gathered in

regional Forest Inventory and Analysis (FIA) studies (Shaw et al. 2005) and in local studies (Eager 1999, Breshears et al. 2005) document variable mortality in Colorado piñon (*Pinus edulis* Englem.) and single-needle piñon (*P. monophylla* Torr. & Frem.) that far exceeds levels measured under climatic conditions prior to the onset of the recent drought (1996 to present). Less-severe mortality has occurred in Utah juniper (*Juniperus osteosperma* (Torr.) Little) and one-seeded juniper (*J. monosperma*) populations (Gitlin et al. 2007). Differential mortality may shift dominance to juniper species and displace vegetative ecotones (Allen and Breshears 1998). Other effects include potential losses of piñon-dependent flora, ectomycorrhizae, and numerous vertebrate species (Mueller et al. 2005). Although drought periods lasting several months have occurred since 2003, and continue until the present time, the presence of pinyon ips related mortality decreased precipitously after 2005.

Protection of the Southwest's extensive piñon–juniper woodlands against drought-induced mortality and insect infestations is a common management concern and management actions are often based on stand charac-
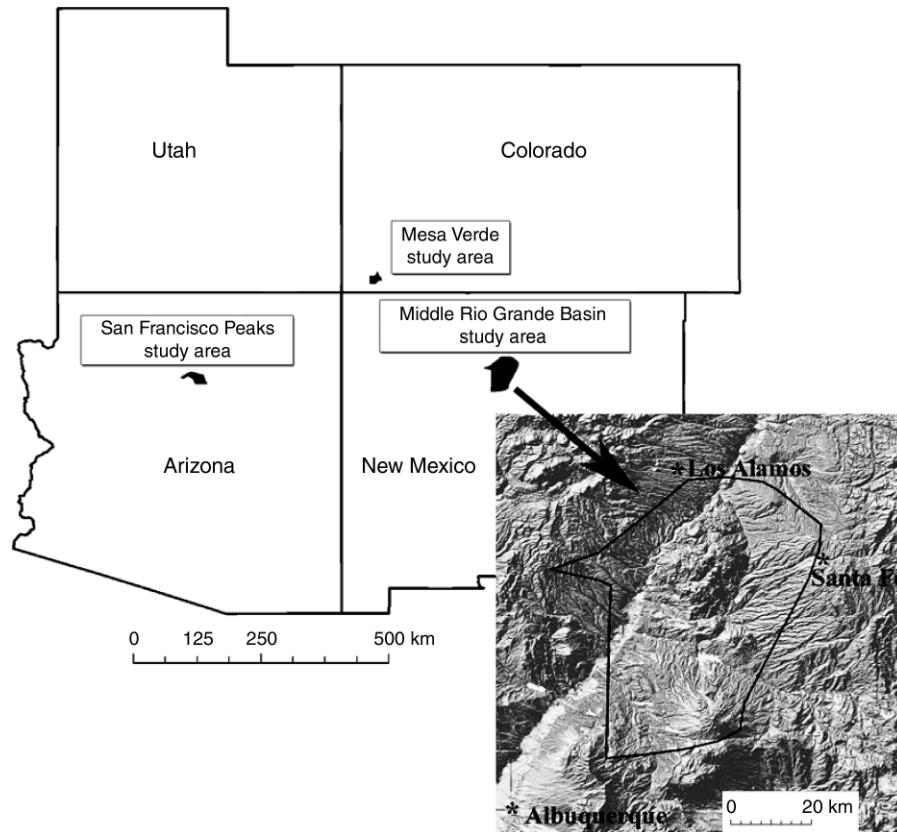
FIG. 1. Locations of study areas in the southwestern United States; black polygons reflect the extent of each study. The Colorado study is located in Mesa Verde National Park, the Arizona study is on the San Francisco Peaks, and the New Mexico study is in the Middle Rio Grande Basin (the inset shows the extent of topography in this expansive study area).

teristics and measures of stand condition (Romme et al. 2007). Current conditions in piñon–juniper woodlands span a wide array of stand structural characteristics and a wide range of densities (Swetnam et al. 1999, Tausch 1999, West 1999, Romme et al. 2007). Heterogeneity of stand densities is at least in part due to variation in prehistoric and recent fire cycles (Romme et al. 2003, Baker and Shinneman 2004) and land use practices (Gifford 1987, Miller and Tausch 2001, Hastings et al. 2003).

Shaw et al. (2005) suggested that infestation may be predicted in part by structural features of the woodland. Negron and Wilson (2003) found a strong relationship between piñon mortality and a tree density index early in the recent drought cycle (1997–1998) with increasing mortality in more dense stands. Fettig et al. (2007) included piñon–juniper woodlands in a review of silvicultural treatments relating stand characteristics to bark beetle infestations. Yet, few other studies have addressed the influence of tree size distribution or the effect of tree density on piñon and juniper mortality, and none have done so after exposure to a decade of extremely dry and hot conditions.

We compare three areas in the Southwest where long-term monitoring of woodland structure and condition

has been on-going for about two decades. We confined our study to stands co-dominated by *P. edulis* (hereafter referred to as "piñon"), and either Utah juniper (*J. osteosperma*) in the Colorado study area or one-seeded juniper (*J. monosperma*) in the New Mexico and Arizona study areas (hereafter referred to as "juniper" when we make statements about both juniper species). Over this range of sites we asked the following: (1) What was the extent of mortality in piñon and in juniper after a prolonged drought (beginning in 1996) and did this vary among three sampled locations? (2) Within a stand, are trees of particular size classes equally susceptible to drought-induced bark beetle outbreaks (piñon) or the direct effects of drought (juniper)? (3) Does tree density and/or basal area influence the severity of mortality during this prolonged drought?

METHODS

Study areas and sampling

Three study areas were established; one in southwestern Colorado, one in northern Arizona (see Plate 1), and one in north-central New Mexico (Fig. 1). The Colorado and Arizona study areas are long-term study sites, established prior to the 1996 initiation of the current

PLATE 1. Tree mortality in northern Arizona, USA. Shown here are skeletons in 2006 of trees that died in 2003. Photo credit: N. S. Cobb.

regional drought. Each woodland experienced different levels of pinyon ips activity (Breshears et al. 2005). Thus, the current study areas were not biased by stand-level mortality. Data from all three studies were collected during the same years (2004 and 2005), using comparable methods. The studies differed slightly in the sampling design and the number and placement of sample plots. The New Mexico study spanned a larger area than did the Colorado or Arizona studies.

We recorded locations with a Trimble Geoexplorer Global Position System (Trimble Navigation Limited, Sunnyvale, California, USA). Within sample plots we recorded the number of dead and live trees of each conifer species (*P. edulis* and *J. osteosperma* or *J. monosperma*). We searched diligently for evidence of possible mortality agents; however despite the probability that other insects or fungi were present, all of the dead piñons except seedlings and smaller samplings had evidence of pinyon ips and we could not identify any insect on junipers. Diameter was collected at base of each live and dead tree (diameter at root collar, drc) because trees often branch near the ground surface. Tree density was calculated as number of all individuals per 100 m². The basal area of each tree was calculated as ba = (drc/2)²π. Basal areas were summed for each plot and expressed for all trees in a plot as m²/ha. Mortality of recently killed trees (i.e., those killed in the current drought period since ca. 1996) was calculated for three size classes: seedling/saplings had diameter at root collar (drc) 0–1.5 cm, pre-reproductive trees had drc 1.6–9.0 cm, and reproductive trees had drc >9.0 cm. Pre-reproductive trees may occasionally produce both pollen and seed cones, but typically do not consistently produce viable cone crops.

Mesa Verde National Park, Colorado.—The Colorado study was located in Mesa Verde National Park in southwest Colorado. Twenty-four study sites had been established in the mid-1990s, before the current drought, as part of a long-term study evaluating woodland structure and health, and representing a range of elevation and soil types. These 24 sites were relocated in 2005 for the current study: 19 were within the National Park Service boundary and five were on Ute Mountain Ute reservation land. At each site, six 15 × 15 m plots were established, creating a belt 30 m wide and 45 m long (1350 m²). Tree species included piñon and Utah juniper.

San Francisco Peaks, Arizona.—The Arizona study was located on the north side of the San Francisco Peaks. Fifty-three sample locations were established between 1998 and 2002. Locations were randomly chosen from maps to ensure they encompassed the elevation range of piñon–juniper woodlands across the entire north face of the San Francisco Peaks. At each location, a plot 10 m wide and 200 m long was established, and divided into 20 100-m² subplots. We sampled alternate 100-m² subplots, and combined the data from the 10 subplots sampled. Sites were visited during the summer and fall of 2004. Subsequent visits in 2005 indicated little to no additional mortality. The tree species included piñon and one-seeded juniper.

Middle Rio Grande Basin, New Mexico.—The New Mexico study was located in the Middle Rio Grande Basin in north-central New Mexico. Thirty-two locations in piñon–juniper woodlands were randomly selected and sampled during the summer of 2005. Locations were chosen by the proximity to a road (>50 m and <1 km), and the proximity to other randomly selected sites (>5 km from another site). Three 100-m² plots were established at each location in a triangular formation, 75 m apart. The tree species included piñon and one-seeded juniper.

Statistical analyses

We summarized descriptive data for site characteristics and mortality patterns in three size classes defined above for each tree species. In order to determine factors influencing mortality, we calculated a binomial response variable defined as the proportion of each species that died (dead piñon/total piñon or dead juniper/total juniper). Independent variables were tree size class, tree density, and stand basal area. In the analysis, mortality of piñon and juniper were considered separately. Because the response was a calculated proportion and not normally distributed, we analyzed the data with logistic regression using general linear mixed model (GLIMMIX procedure) in SAS software (Littell et al. 2002, SAS Institute 2003). The experiment was executed as a split plot in a completely randomized design. The main plot design was a completely randomized (one-way) layout consisting of three "areas" (New Mexico, Colorado, and Arizona) with a total of 109 "plots" randomly located within appropriate woodlands over the three areas. Both

TABLE 1.   Descriptive information for comparative purposes of three study areas in Colorado, New Mexico, and Arizona, USA, with regard to elevation and site configuration.

	Study areas		
Parameter	Colorado	Arizona	New Mexico
Elevation (m; mean ± SE)	2199 ± 23	2040 ± 18	2036 ± 19
Sample size (no. plots)	24	53	32
Sample area (ha)	3.24	5.30	9.60
Site area (km²)	214	189	2245

area and plot nested within area were treated as random effects in the generalized linear mixed model. Tree size (seedling/sapling, pre-reproductive, reproductive) was considered a fixed split of the main plots. Total basal area and tree density were included as covariates. The binomial distribution was used to model the proportion of mortality, using the canonical or standard logit link function (logit link function is the function that linearizes probabilities, i.e., $\text{logit}(P) = \log(P/[1 - P])$) (Hosmer and Lemeshow 2000). Specific sources of variability (with their degrees of freedom) in the final model are as follows: area ($3 - 1 = 2$, a random effect but part of design), plot ($106 = [53 - 1] + [24 - 1] + [32 - 1]$; 53, 24, and 32 are the number of plots in Arizona, Colorado, and New Mexico, respectively), tree size ($3 - 1 = 2$; sapling, immature, mature size classes), and area × tree ($2 \times 2 = 4$; also random because area is random).

RESULTS

Comparison among site characteristics and mortality patterns

Sites were located in Colorado, Arizona, and New Mexico, representing a spectrum of piñon–juniper woodland structural conditions. All sites had a similar range of elevations and plot area sampled (Table 1). Stand structure differed regionally (Table 2); generally, the New Mexico woodland was a dense thicket of small trees, the Colorado site was intermediate in density and consisted of old-growth structure (Floyd et al. 2004) and the Arizona site had the lowest tree density but exhibited the highest basal area due to the number of large junipers (Table 2).

In all three sites, the most common immediate cause of death in piñon was pinyon ips, *Ips confusus*, as evidenced by galleries and pitch-filled entrance holes on most dead adult piñons. The New Mexico plots contained the highest piñon mortality, whereas the Colorado site had the least. At the Colorado site, mortality did not differ significantly across site conditions geologic type, soil depth or precipitation (M. L. Floyd, *unpublished data*). Mortality was described in seedling/sapling, pre-reproductive, and reproductive trees at each of the three study areas. Piñons were most heavily affected by pinyon ips in reproductive trees with mortality averaging 60% in Colorado, 74% in Arizona,

and 94% in New Mexico study areas. Smaller size classes are also affected although to a lesser degree (Fig. 2). There was considerable piñon mortality in seedlings/ saplings in Arizona but not in the other two study areas. The highest mortality in pre-reproductive and reproductive trees occurred at the New Mexico location.

Logistic regressions.—Many GLIMMIX analysis of covariance models were tried (Cleveland et al. 1992); the formulation depicted in Figs. 3 and 4 represents the best fit. In no case were we able to predict the mortality of juniper from the independent variables selected (tree size class, stand basal area or tree density); this is likely due to low mortality of juniper overall. However, data on piñon mortality were available in 246 of the 271 plots. Tree size class was not a statistically significant influence on piñon mortality ($F = 4.49$, df = 2, 2, $P = 0.18$) but seems to slightly improve the model fit as measured by the generalized chi square/df (5.39 vs. 6.55). (Note: this measure of fit is high if we consider a good fit to have a chi-square/df approaching 1.) Tree size also slightly improved the pattern of residuals. ANOVA results for Type III tests of fixed effects suggest that while there appears to be no significant influence of tree size, there is a significant relationship of mortality with tree density ($F = 40.2$, df = 1, 236, $P < 0.0001$) and basal area ($F = 91.8$, df = 1, 236, $P < 0.0001$). The generalized chi-square for this final model, is 1293.08 with a generalized chi-square/df value of 5.39.

In order to visualize these effects on piñon pine mortality, trellis plots (Cleveland 1993) were created (Fig. 3) in which the dotted line is the linear regression fit and the solid line is a Loess smoothing fit (Cleveland and Devlin 1988). (Loess is a smoothing function that allows the underlying relationship between the predictor and response variable to be estimated using local polynomials to fit the data. Loess does not force the fit to be

TABLE 2.   Woodland characteristics and mortality patterns among three study areas.

	Study areas		
Stand attribute	Colorado	Arizona	New Mexico
Juniper density (trees/ha)	402 ± 53	196 ± 29	494 ± 47
Piñon density (trees/ha)	740 ± 74	391 ± 48	1005 ± 142
Tree density (trees/ha)	1142 ± 113	684 ± 71	1578 ± 177
Juniper basal area (m²/ha)	15.04 ± 1.63	18.13 ± 3.32	12.59 ± 2.21
Piñon basal area (m²/ha)	9.67 ± 1.32	4.16 ± .71	1.21 ± .20
Tree basal area (m²/ha)	25.05 ± 2.09	27.30 ± 3.59	16.74 ± 23.13
Juniper mortality (%)	9 ± 1.67	10 ± 2.23	3 ± 0.80
Piñon mortality (%)	32 ± 4.50	52 ± 4.24	65 ± 4.18

Notes: Piñon is *Pinus edulis*; Juniper is *Juniperus monosperma* in New Mexico and Arizona, and *J. osteosperma* in Colorado. Values are means ± SE.
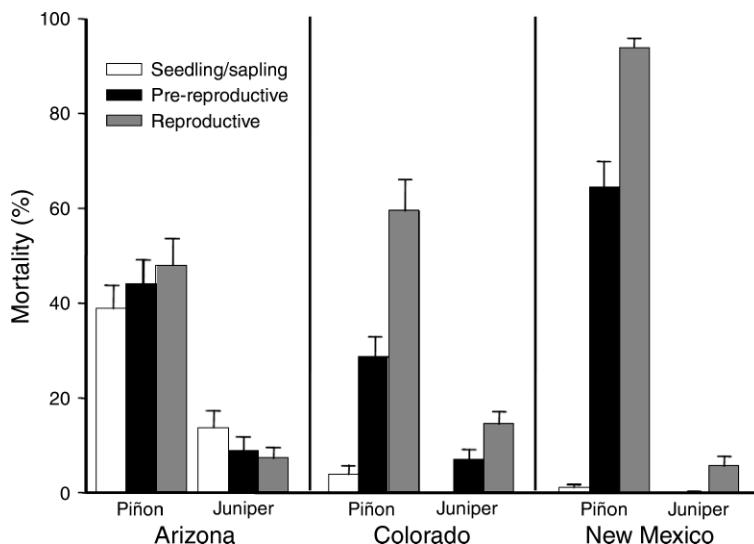
FIG. 2. The percentage of each size class killed during the 2002–2005 drought period for piñon (*Pinus edulis*) and juniper (*Juniperus monosperma* in the New Mexico and Arizona study areas, *J. osteosperma* in Colorado; values are means + SE). Seedlings and saplings are defined as having 0–1.5 cm drc (diameter at root collar); pre-reproductive trees have 1.6–9.0 cm drc; reproductive trees have >9.0 cm drc.

linear, quadratic, etc., but allows for the extraction of expression of a nonlinear "signal.") For piñon, in which the model has significance, the trend in each site is irregular, yet the Loess curves suggest a generally declining mortality as a function of tree density or stand basal area increases (up to basal areas of about 6 m²/ha There are really too few points (i.e. inadequate support) for modeling beyond a basal area of 6 m²/ha. Trellis plots for each piñon size class (Fig. 4) show similar trends in response to density with one exception; the response of the smallest size class to basal area shows rather a generally increasing mortality with increasing total basal area (Fig. 4A).

Although the terms in the piñon mortality model are statistically significant, the model was still very "noisy"

and any predictions have very wide confidence intervals. For example, a 95% confidence interval for the average probability of piñon mortality for seedlings–saplings at the average of the two covariates is (0.20, 0.81). Similarly, confidence intervals for pre-reproductive and reproductive trees are respectively (0.25, 0.67) and (0.59, 0.89). Thus, we are cautious in interpreting or over-stating the causes of mortality trends.

DISCUSSION

Droughts of the past decade caused significant mortality of dominant conifers between 1650 and 2400 m of elevation in the southwestern United States due in part to soil moisture depletion and high temperatures (Breshears et al. 2005, Shaw et al. 2005). While twig
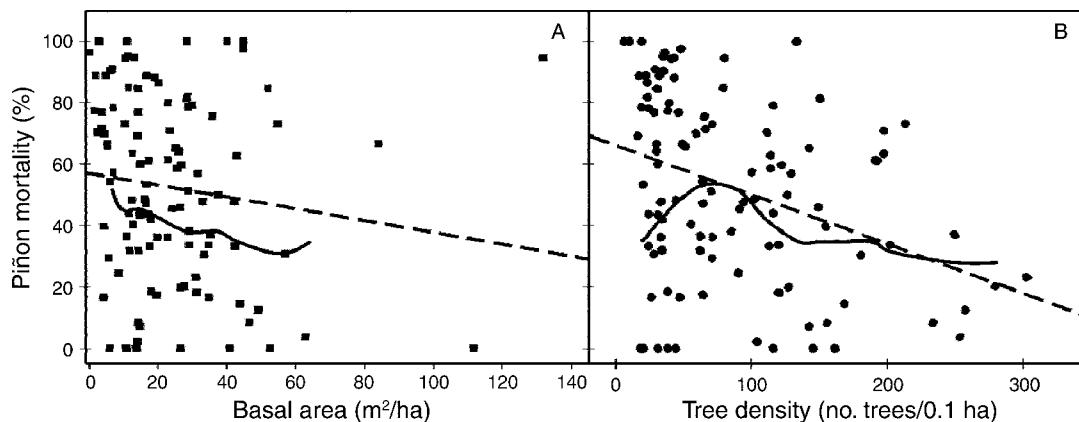
FIG. 3. Influence of (A) total basal area and (B) tree density (total trees/ha) on piñon mortality. Dashed lines represent linear regression lines, while solid lines represent the Loess smoothing curves. Note the declining trend in piñon mortality with increased basal area with linear regression, and an initial rise, then fall with the Loess curve.
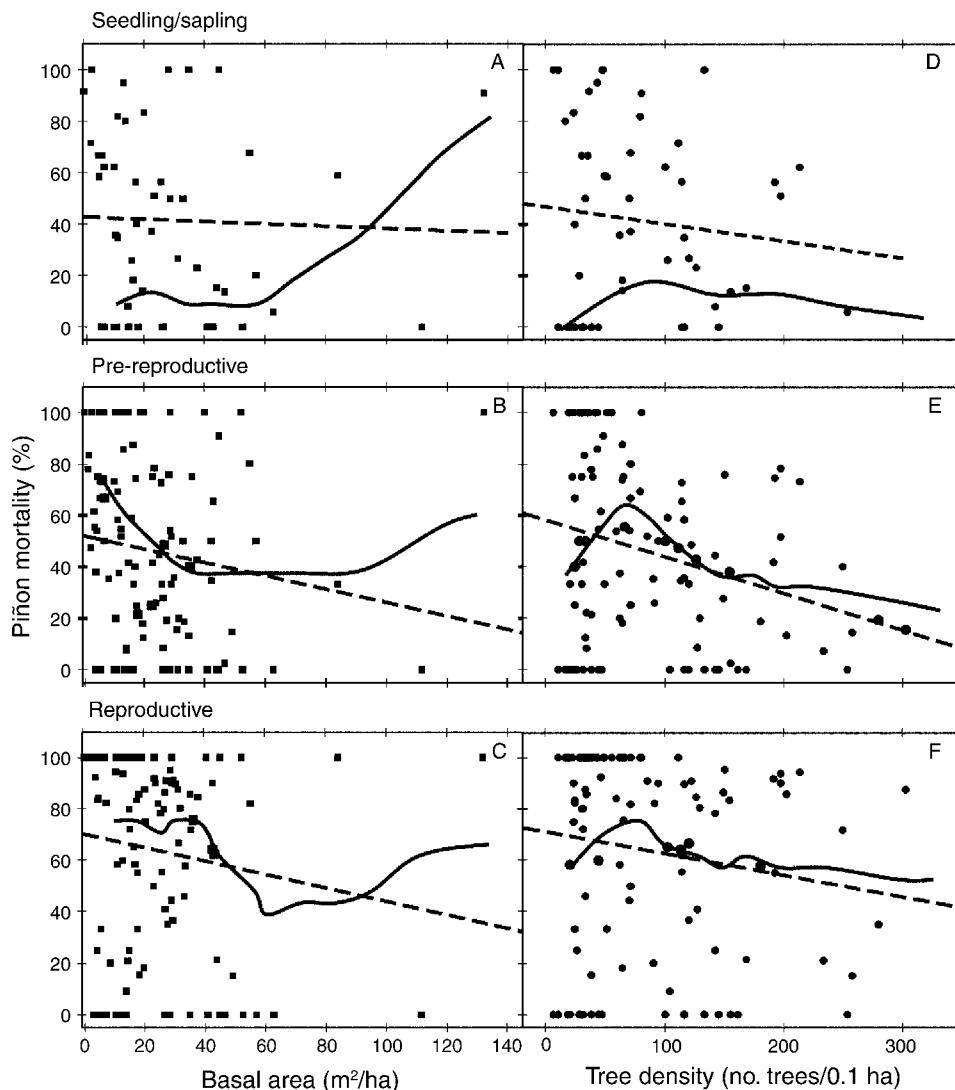
FIG. 4. (A–C) The influence of total basal area on piñon mortality in three size classes (seedling/sapling, 0–1.5 cm drc; pre-reproductive, 1.6–9.0 cm drc; and reproductive, >9.0 cm drc). (D–F) The influence of tree density (total trees per 0.1 ha) on piñon mortality in the same three size classes. Dashed lines represent linear regression lines, while solid lines represent Loess curves.

beetles (*Pityophthorus* sp.), pitch mass borer (*Dioryctria ponderosae* Dyar), dwarf mistletoe (*Arceuthobium* sp.), piñon needle scale (*Matsococcus acalyptus* Herbert), and pinon blister rust are also common agents of stress and mortality in piñon populations in all three locations (for others, see Leatherman and Kondratieff 2003), the current regional die-off of piñon has been attributed primarily to explosion of pinyon ips bark beetles (Negron and Wilson 2003, Mueller et al. 2005, Shaw et al. 2005). In southwestern Colorado, including the Mesa Verde location), black stain root disease (*Ophiostoma wageneri* Goheen and Cobb) has been an important mortality agent during the last century; while present in the Mesa Verde study area, all dead trees in the plots also had evidence of pinyon ips. Other insects and fungi may weaken trees, predisposing them to pinyon ips

infestation (Kearns and Jacobi 2005). Although we searched diligently for evidence of all of these agents in three southwestern study areas, pinyon ips was present on nearly all of the dead pinons (except seedlings) in this study, and although other agents (such as black stain root disease) are present in the area, their effects were masked by the widespread beetle kill. Also, while cedar mistletoe (*Phoradendron juniperinum* Engelmann.), *Gymnosporangium* rusts and *Phloeosinus* bark beetles, can be important stressors or mortality agents for juniper, we could not locate them in our study areas, therefore we concluded that in these three locations, juniper die-off was primarily due to direct effects of the prolonged drought.

Regional variation in mortality occurred in our three study locations, with the greatest overall mortality in

New Mexico and the least in Colorado. At all sites, piñon mortality was greatest in older, reproductive trees, ranging from 60% to 94%. Juniper mortality was much lower than piñon mortality at all sites and no pattern in size class susceptibility was apparent.

Logistic regression modeling was unsuccessful in predicting the likely causes of juniper mortality, finding no relationship of mortality to tree density or basal area. While we detected a significant relationship in piñon mortality with basal area and density, that relationship was erratic in mid range and then declined at higher densities or greater basal area. We are cautious in interpreting these trends because of wide confidence intervals surrounding the predicted mortality. However, the data do not support a trend of increased stress (weakening of tree defenses) as density or basal area rises.

A number of forest trees, including ponderosa pine and Douglas fir (*Pseudotsuga menziesii*), have been shown to exhibit density-dependent increases in susceptibility to insects often attributed to declining tree health imposed by resource limitations (Skov et al. 2004, Wallin et al. 2004, Fettig et al. 2007). In piñon–juniper woodlands of Arizona, Negron and Wilson (2003) detected a strong positive relationship of piñon mortality with a tree density index. They suggested that higher densities increased stress factors, reducing vigor (perhaps by reducing growth rates and altering carbohydrate mobility), thereby increasing susceptibility to pinyon ips.

Differences in our data and those previously documented may be attributed, in part, to length of drought exposure. Because trees in our three regions had been subjected to declining water availability and warmer temperatures for at least four additional years and the pinyon ips epidemic had become much more severe over time throughout the Southwest (Eager 1999, Breshears et al. 2005, Shaw et al. 2005), it is possible that the density-dependent trend documented by the earlier study (Negron and Wilson 2003) was superseded by extreme drought effects, masking any previously documented density trends.

The range of natural variation in piñon–juniper densities is broad across the Southwest, varying with site conditions such as soil depth, elevation, precipitation (e.g., West 1999), responses to the relatively wet 1900s (Swetnam et al. 1999), and land use history such as fire or grazing (e.g., Tausch 1999). For example, on Anderson Mesa in Arizona, piñon–juniper woodlands may have experienced historic density increases since the late 1800s (Landis and Bailey 2005), but in southwest Colorado where fire intervals span centuries (Floyd et al. 2004), woodlands have experienced stable densities over historic periods (Romme et al. 2003). To account for this breadth in natural variation in piñon–juniper woodlands, our study compared woodlands representing a wide span in tree density and site characteristics (Table 1) yet, each site lacks a density-dependent response under prolonged drought conditions. Given climate

projections for the Southwest that include increasing aridity and rising temperatures (Seager et al. 2007), as well as globally increasing extreme events (Easterling et al. 2000), it is critical that we expand our understanding of responses by the widespread piñon–juniper woodlands to prolonged drought and insect infestations. In addition, insight into the relationship of site potential and productivity to infestation rates may be useful. Such understanding will be critical for informed management responses to climate change.

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