

Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona, USA

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ARTICLE INFO

Article history:

Received 2 September 2010
Received in revised form
28 September 2010
Accepted 29 September 2010

Keywords:

Climate change
Drought
Gambel oak
Mortality
Quaking aspen
White fir

ABSTRACT

We monitored tree mortality in northern Arizona (USA) mixed-conifer and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) forests from 1997 to 2007, a period of severe drought in this area. Mortality was pervasive, occurring on 100 and 98% of 53 mixed-conifer and 60 ponderosa pine plots (1-ha each), respectively. Most mortality was attributable to a suite of forest insects, mediated by drought stress. The number of trees dying from 2002 to 2007 was more than 200% greater than the number dying from 1997 to 2002 in mixed-conifer forest and 74% greater in ponderosa pine forest. Extent of mortality was spatially variable in both forest types. Median cumulative mortality (the ratio of dead to live trees) increased by approximately 53 and 65% in mixed-conifer and ponderosa pine forests, respectively, from 2002 to 2007. Median mortality rates from 2002 to 2007 were approximately 2.0% year⁻¹ in mixed-conifer forest (range = 0–28.5%) and 0.4% year⁻¹ in ponderosa pine forest (range = 0–13.6%). Mortality rates generally were not strongly related to either elevation or stand density. Mortality was nonrandom with respect to tree size classes and species. Proportions of trees dying were greatest in the largest size classes, particularly in mixed-conifer forest, where mortality in the largest size class exceeded 22% from 2002 to 2007. Mortality in mixed-conifer forest was particularly pronounced for quaking aspen (85%) and white fir (28%), the least drought tolerant species present. These results provide an early glimpse of how these forest types are likely to respond to predicted climate changes in the southwestern USA. They suggest that these forests are not resilient to climate change, and that treatments to increase resilience to climate change may be appropriate. Research on causes of spatial heterogeneity in extent of mortality might suggest valuable approaches to aid in increasing resilience.

Published by Elsevier B.V.

1. Introduction

There is strong evidence that global climates are changing in response to increasing emissions of greenhouse gases (e.g. IPCC, 2007), and that changing climates are affecting forest ecosystems throughout the world either directly or indirectly through altered disturbance regimes (e.g., Bonan, 2008; Raffa et al., 2008; Breshears et al., 2009; Floyd et al., 2009; Negron et al., 2009; van Mantgem et al., 2009; Allen et al., 2010). Understanding the effects of climate change on forests is critical to informing current forest management and conservation planning for the future (Allen et al., 2010).

Because relative effects of climate change may vary among forest types, specific information is needed to understand how particular forest types will respond to changing climates. As part of a study of snag (standing dead trees) dynamics, we monitored tree mortality in mixed-conifer and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) forests in northern Arizona from 1997 to 2007.

This interval overlapped with a period of severe, global-climate-change type drought (defined here as a drought accompanied by warmer temperatures; Breshears et al., 2005) in this area (McPhee et al., 2004; Mueller et al., 2005; Hereford, 2007; Floyd et al., 2009), providing a unique opportunity to monitor patterns in drought-mediated tree mortality in these forest types. Previous studies documented extensive mortality in pinyon (*Pinus edulis* Engelm.)–juniper (*Juniperus* spp.) woodlands (Breshears et al., 2005; Mueller et al., 2005; Floyd et al., 2009) and ponderosa pine forest (Negron et al., 2009) in this region, but similar information is lacking for area mixed-conifer forests. Ganey and Vojta (2005) summarized changes in snag populations from 1997 to 2002 at our study sites, but they captured mortality only during the early and less-severe phase of this drought and did not relate mortality to numbers of live trees. Here, we quantify accelerated tree mortality that occurred from 2002 to 2007 during a period of continuing drought. Specifically, we estimate tree mortality rates and cumulative mortality (Stephens and Gill, 2005) in these forest types, and summarize patterns of tree mortality relative to composition of live tree populations and relative drought tolerance of tree species. These data provide an early glimpse of trends in northern Arizona

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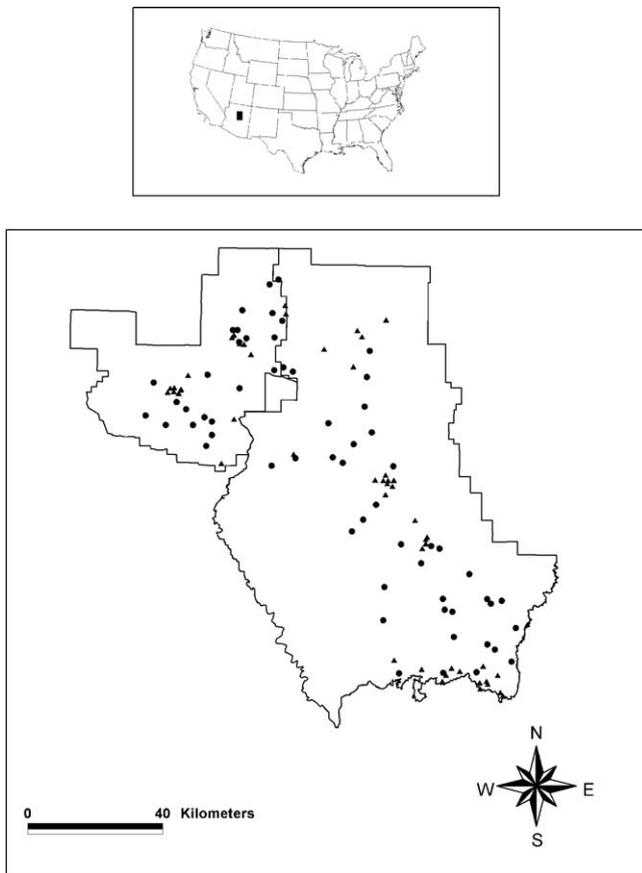


Fig. 1. Location of the study area (black box, top) in northern Arizona, USA, and locations of snag-monitoring plots within the study area (bottom). Plots were located in the Coconino (right) and Kaibab (left) National Forests, north-central Arizona. Plots in ponderosa pine forest ($n=60$) are indicated by circles, plots in mixed-conifer forest ($n=53$) by triangles.

forests likely under the most plausible global climate change scenario of increasing temperatures and aridity in the southwestern United States (Seager et al., 2007).

2. Study area

The study area encompassed approximately 73,000 ha in north-central Arizona (Fig. 1). Within the study area, study plots were randomly located in mixed-conifer ($n=53$ plots) and ponderosa pine (*P. ponderosa* Dougl. ex Laws; $n=60$ plots) forests (Ganey, 1999). Mixed-conifer forests were dominated numerically by ponderosa pine, white fir (*Abies concolor* Lindl. ex Hildebr.), and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), which together accounted for approximately 90% of total trees sampled in this forest type. Other species included Gambel oak (*Quercus gambelii* Nutt.), quaking aspen (*Populus tremuloides* Michaux), and limber pine (*P. flexilis* James), in that order of frequency. Ponderosa pine accounted for over 90% of trees in ponderosa pine forest. Gambel oak also was relatively common (approximately 8% of total trees by frequency), and alligator juniper (*Juniperus deppeana* Steud), Douglas-fir, quaking aspen, limber pine, pinyon pine, and other species of juniper were present in small numbers in some stands.

The study area included a wide range in topography. Ponderosa pine plots ranged from 1778 to 2561 m in elevation, and mixed-conifer plots ranged from 1886 to 2720 m. These plots thus represented the entire elevational range of these forest types within this area, from the transition zone between pinyon–juniper woodland and ponderosa pine at lower elevations to the ecotone

between mixed-conifer and Engelmann spruce (*Picea engelmanni* Parry ex Engelm.)–corkbark fir (*Abies lasiocarpa* var. *arizonica* [Merriam] Lemmon) forests at higher elevations (Brown et al., 1980). In addition, plots included both commercial forests and administratively reserved lands such as wilderness and other roadless areas.

3. Methods

Sampling was conducted on a set of randomly located plots originally established in 1997 to monitor dynamics of snag populations (Ganey, 1999). We established plots using a stratified random sampling procedure with forest type and Ranger District as strata. Ranger Districts ($n=6$) were included as strata to ensure adequate geographic representation throughout the study area. We selected stands by: (1) querying the stand data base for the Coconino and Kaibab National Forests to generate a list of stands by forest type and Ranger District; (2) selecting all stands from this list with stand area >10 ha (to facilitate locating plots within stands while avoiding stand boundaries); and (3) randomly selecting 10 stands from this list in each forest type (mixed-conifer, ponderosa pine) on each Ranger District. Boundaries of selected stands were then plotted on 1:24,000 topographic maps.

To establish plots in the field, we located the approximate centers of mapped stands in the field using topography, visual landmarks, and a global positioning system (GPS) unit (Trimble Geo Explorer). We then used a compass to select a random azimuth and number of paces (number of paces = azimuth/10, and thus ranged from 1 to 36), and located the first plot corner by walking the indicated number of paces in the indicated direction. From this corner, we selected another random azimuth as above, and laid out one side of the plot along that azimuth (plot dimensions = $100\text{ m} \times 100\text{ m}$, area = 1 ha). Upon reaching the second plot corner, we used a coin flip to determine whether to turn left or right, then the second plot boundary was laid out on an azimuth perpendicular to the original azimuth. The square was then closed to complete plot layout.

We marked the first plot corner with a metal stake, and recorded differentially corrected GPS coordinates to aid in relocating the stake for re-sampling of plots through time. We sampled all snags ≥ 2 m in height and ≥ 20 cm in diameter at breast height (dbh) in 1997, 2002, and 2007. All snags were uniquely marked with numbered metal tags, allowing us to distinguish existing snags from new snags when re-sampling plots.

We sampled all live trees ≥ 20 cm dbh in a 0.09-ha subplot ($30\text{ m} \times 30\text{ m}$) within each snag plot in 2004. We reduced plot size for tree sampling because live trees were far more abundant than snags and time constraints precluded sampling trees on the entire 1-ha plot. We did not sample trees < 20 cm dbh for consistency with snag-sampling methods; note that this results in underestimates of stand density and basal area. For all trees and snags sampled we recorded species and dbh to the nearest cm. Trees were temporarily marked with chalk to avoid double-sampling of individual trees.

No plots underwent commercial timber harvest between 1997 and 2007. Three ponderosa pine plots underwent thinning of smaller trees during this period, and two ponderosa pine plots underwent prescribed fire. We included these plots here because (1) our estimates of mortality were based on direct observations of standing dead trees and did not include trees removed by thinning, (2) field observations indicated that the prescribed fires killed very few trees ≥ 20 -cm dbh on the plots affected, and (3) our objective was to evaluate mortality across the landscape, including areas subjected to thinning and prescribed burning. We excluded plots that experienced intense wildfire (two in mixed-conifer and three in ponderosa pine forests) when estimating and comparing mortality parameters, because (1) these fires killed large numbers of trees

Table 1
Mortality scenarios used to estimate live tree densities in 2002 and 2007, using data on live tree density collected in 2004 and observed numbers of snags recruited from 2002 to 2007.

Scenario	Estimating equations		
	Assumptions	2002 tree density	2007 tree density
1	All mortality 2002–2004 No tree ingrowth 2004–2007	=2004 tree density + all snags recruited	=2004 tree density
2	Mortality constant 2002–2007 No tree ingrowth 2002–2007	=2004 tree density + (0.4 × snags recruited)	=2004 tree density – (0.6 × snags recruited)
3	All mortality 2004–2007 No tree ingrowth 2002–2004	=2004 tree density	=2004 tree density – all snags recruited

in these plots, and (2) more importantly, intense wildfire melted the metal tags used to mark snags (Ganey and Vojta, 2005), making it difficult to determine whether dead trees represented new mortality or pre-existing snags.

We summarized data on mortality patterns within both forest types. We present medians and ranges as estimates of central tendency and variability because distributions were often so highly skewed that a few plots greatly influenced mean estimates.

Several analyses (discussed below) required estimates of live tree density in 2002, 2007, or both years. Because we sampled trees in a subplot within snag plots and only sampled trees in 2004, we had both spatial and temporal scale issues to confront. We addressed differences in spatial scale by converting live tree numbers to density (numbers ha⁻¹) to standardize them relative to snag numbers. To address temporal issues, we estimated tree density in 2002 and 2007 based on the 2004 sample of trees adjusted by counts of snags recruited from 2002 to 2007. Because we were uncertain exactly when snags were recruited within this interval, we used three mortality scenarios in estimating tree numbers. This allowed us to bracket the results, and to evaluate the effect of extreme assumptions on results.

Scenario one assumed that all snags recruited from 2002 to 2007 died before trees were sampled in 2004. Scenario 2 assumed that snags were recruited at a constant rate between 2002 and 2007 (i.e., 40% of the observed mortality occurred prior to tree sampling and 60% of the observed mortality occurred after trees were sampled). Scenario 3 assumed that all mortality occurred after trees were sampled in 2004. Equations used for density estimates are shown in Table 1.

Because all of these scenarios are based on assumptions, estimates of tree densities in 2002 and 2007 are only approximate, and any analyses involving these estimates also are only approximate. Nevertheless, we view the resulting analyses as useful in understanding patterns of tree mortality, especially because the assumptions may not be violated greatly over the 2- and 3-year time periods required for these estimates. We did not extrapolate tree densities back to 1997, because the assumptions required become less tenable as the time line increases.

We estimated cumulative mortality as the ratio of all standing snags to live trees expressed as a percentage (Stephens and Gill, 2005) in 2002 and 2007 by forest type. Note that this parameter is a point estimate involving all dead trees, regardless of when they died, and can exceed 100% where dead trees outnumber live trees. We calculated approximate tree mortality rates for the period from 2002 to 2007 as (Stephens and Gill, 2005):

$$m = 1 - \left(\frac{N_1}{N_0} \right)^{1/t}, \quad (1)$$

where N_0 and N_1 are counts of trees at the beginning and end of the measurement interval t .

We used Wilcoxon signed-ranks tests (Conover, 1980) stratified by forest type to compare numbers of trees dying from 1997 to 2002 with numbers dying from 2002 to 2007, and to compare estimates

of cumulative mortality in 2002 with estimates in 2007. We used plot as the pairing factor in all tests. We evaluated potential relationships between live tree density, species composition, elevation, and mortality rates using Pearson's product-moment correlation coefficient (Zar, 1984:307).

We compared composition of trees dying from 2002 to 2007 (species and size-class distribution) to composition of live tree populations (a measure of availability) using chi-square tests for heterogeneity (Conover, 1980). We also evaluated relative mortality as a function of drought tolerance, using a species-specific drought-tolerance index developed by Niinemets and Vallardes (2006). This index is based on physiological tolerance to water stress, morphological and life cycle strategies to cope with scant water, and water availability estimated on the sites where the species frequently occur (Niinemets and Vallardes, 2006:528), and ranges from 0 (no drought tolerance) to 5 (maximal drought tolerance). For all statistical analyses requiring estimates of live tree density, we based those estimates on mortality scenario 2 (Table 1).

4. Results

Density of live trees ≥ 20 cm dbh ranged from 78 to 489 (median = 266.7) trees ha⁻¹ in mixed-conifer forests and from 11 to 689 (median = 227.8) trees ha⁻¹ in ponderosa pine forests, and basal area ranged from 7 to 52 (median = 25.2) m² ha⁻¹ and from 1 to 44 (median = 19.7) m² ha⁻¹ in mixed-conifer and ponderosa pine forests, respectively, illustrating the wide range in forest structural conditions sampled. Tree mortality was widespread, with mortality observed on 100 and 98% of mixed-conifer and ponderosa pine plots from 1997 to 2007, respectively.

More mortality occurred from 2002 to 2007 than from 1997 to 2002. Total tree mortality increased by over 200% in mixed-conifer forest and by 74% in ponderosa pine forest between these time periods (Fig. 2). Extent of mortality was spatially variable in both forest types and time periods, however. Median number of trees dying in mixed-conifer forest increased significantly (Wilcoxon signed-ranks test, $P < 0.001$) from 9.0 ha⁻¹ (range = 1–190) between 1997 and 2002 to 23.0 ha⁻¹ (range = 0–258) between 2002 and 2007. In ponderosa pine forest, median number of trees dying increased significantly (Wilcoxon signed-ranks test, $P < 0.001$) from 1.5 ha⁻¹ (range = 0–125) between 1997 and 2002 to 4.0 ha⁻¹ (range = 0–33) between 2002 and 2007.

Median cumulative mortality increased significantly in mixed-conifer forest (Wilcoxon signed-ranks test, $P < 0.001$) from 11.3% in 2002 (range = 3.6–36.3%) to 21.1% in 2007 (range = 5.5–517.7%). In ponderosa pine forest, median cumulative mortality also increased significantly (Wilcoxon signed-ranks test, $P < 0.001$) from 2.6% in 2002 (range = 0.3–28.4%) to 4.0% in 2007 (range = 0.3–111.0%). Results were relatively robust to differing assumptions about timing of mortality, as estimates of cumulative mortality differed little between mortality scenarios in both forest types in both 2002 and 2007 (Fig. 3).

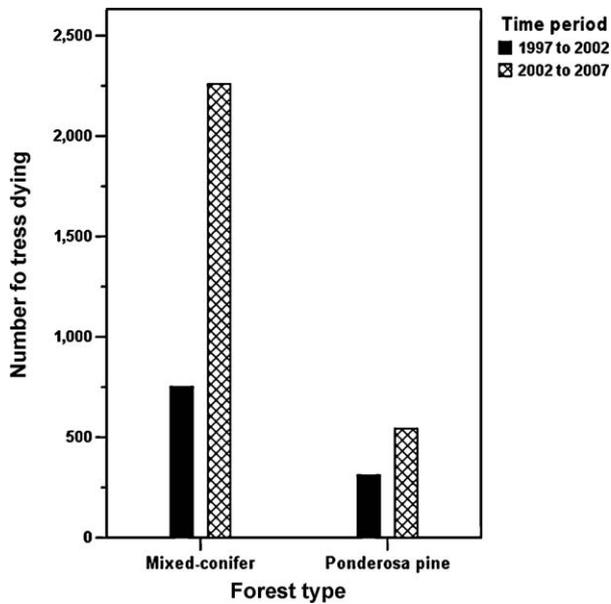


Fig. 2. Number of trees (≥ 20 cm dbh) dying by forest type and time period. Both forest types experienced a large increase in mortality from 2002 to 2007.

Mortality rates from 2002 to 2007 varied widely among plots, ranging from 0 to 28.5% year⁻¹ in mixed-conifer forest (median = 2.0 year⁻¹), and from 0 to 13.6% year⁻¹ in ponderosa pine forest (median = 0.4% year⁻¹). As with cumulative mortality (Fig. 3), mortality rates varied little under different mortality scenarios in both forest types in both years.

Mortality rate was not significantly correlated with either elevation ($P=0.065$) or live tree density in mixed-conifer forest ($P=0.676$), but was positively correlated ($r=0.339$, $P=0.016$) with proportion of live white fir trees in this forest type. No significant relationships were observed between mortality rate and other individual tree species in mixed-conifer forest (all P -values >0.105).

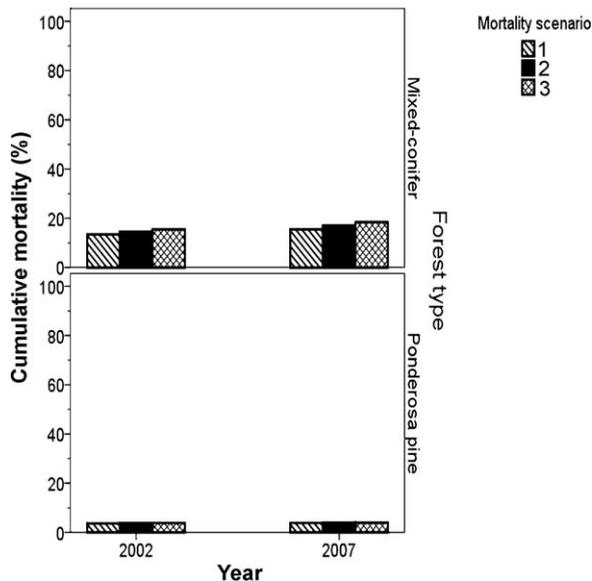


Fig. 3. Cumulative mortality (or ratio of dead to live trees) in northern Arizona mixed-conifer and ponderosa pine forest in 2002 and 2007 under three different mortality scenarios. These scenarios (described in the text and Table 1) differed in assumptions regarding timing of mortality, which in turn influenced estimates of live tree numbers. Estimates shown here were based on all recruited snags and trees within forest types, rather than on plot-level estimates.

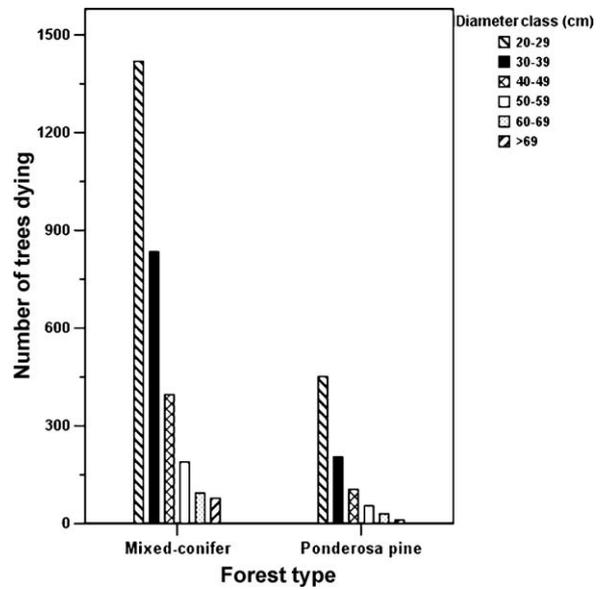


Fig. 4. Number of trees dying by diameter class in northern Arizona mixed-conifer and ponderosa pine forests, 1997 to 2007. Mortality occurred across all size classes, but absolute mortality was greatest in the smaller size classes.

Mortality rate also was not significantly correlated with either elevation ($P=0.549$) or live tree density in ponderosa pine forest ($P=0.112$), and no significant relationships were observed between mortality rates and species composition in ponderosa pine forests (all P -values >0.521).

Mortality occurred in all size classes in both forest types, with most mortality occurring in the smaller size classes (Fig. 4). Diameter distributions of live trees also were heavily dominated by small trees, however, and relative mortality (estimated as % of live trees dying) generally was greater in the larger size classes (Fig. 5). Size-class composition of trees dying from 2002 to 2007 differed significantly from composition of tree populations in 2002 in both

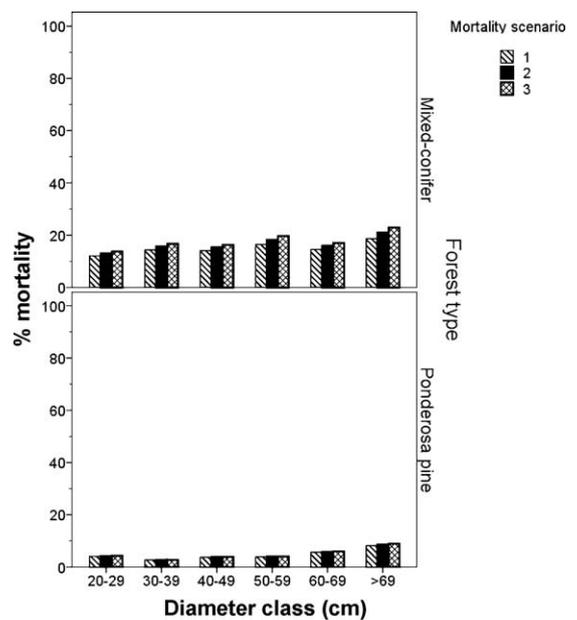


Fig. 5. Relative mortality by tree size class from 2002 to 2007 in northern Arizona mixed-conifer and ponderosa pine forest. Relative mortality was estimated as percent of live trees, with live tree density estimated under three different scenarios describing timing of mortality (see text and Table 1 for details).

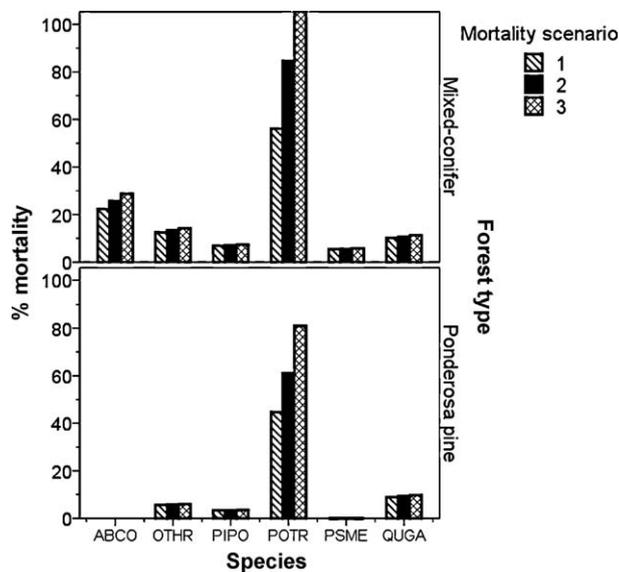


Fig. 6. Relative mortality by tree species in northern Arizona mixed-conifer and ponderosa pine forest, 2002–2007. Species acronyms: ABCO = white fir, PIPO = ponderosa pine, POTR = quaking aspen, PSME = Douglas-fir, QUGA = Gambel oak, and OTHER = all other species. Relative mortality was estimated as percent of live trees, with live tree density estimated under three different scenarios describing timing of mortality (see text and Table 1 for details).

forest types (chi-square tests, both P -values <0.001). In mixed-conifer forest, mortality was lower than expected in the smallest size class, approximately as expected in the second- and third-smallest size classes, and greater than expected in the three largest size classes, relative to size-class composition of tree populations. In ponderosa pine forest, mortality was lower than expected in the two smallest size classes, approximately as expected in the third-smallest size class, and greater than expected in the three largest size classes, relative to size-class composition of tree populations. In both forest types, patterns were similar across all three mortality scenarios, with only slight differences in relative mortality within size classes attributable to different assumptions regarding timing of mortality.

Mortality occurred in all tree species, and relative mortality of all species generally was greater in mixed-conifer than in ponderosa pine forest (Fig. 6). Species composition of trees dying from 2002 to 2007 differed significantly from composition of tree populations in 2002 in both forest types (chi-square tests, both P -values <0.001). Mortality in mixed-conifer forest was greater than expected (based on composition of tree populations) for white fir and quaking aspen, and lower than expected for all other species. Relative mortality was very high for quaking aspen and white fir, with approximately 85 and 28% mortality, respectively (Fig. 6). These were the least drought tolerant species in these forest types (Fig. 7). No other species showed such high proportional mortality in either forest type (Figs. 6 and 7). In ponderosa pine forest, mortality was greater than expected for quaking aspen and Gambel oak and less than expected for ponderosa pine, relative to species composition of live tree populations.

Varying assumptions regarding timing of mortality had little effect on estimates of relative mortality for most species (Fig. 6). Only relative mortality of quaking aspen differed greatly across scenarios. We suspect this occurred because quaking aspen was relatively uncommon in live tree populations. As a result, denominators used in estimating relative mortality were small in all scenarios. All scenarios indicated high relative mortality in quaking aspen, however (range = 45–100% mortality, Fig. 6).

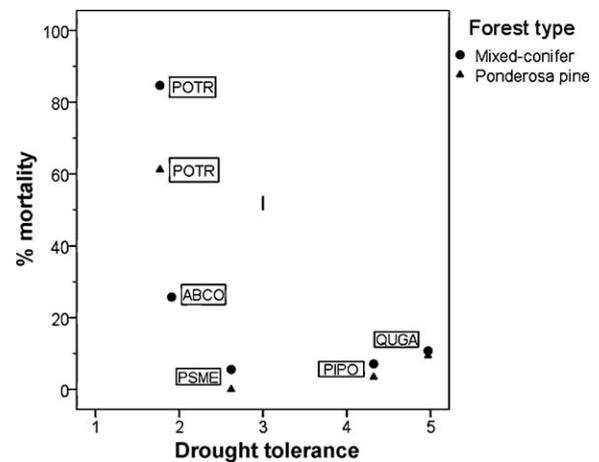


Fig. 7. Relative mortality by tree species from 2002 to 2007 in northern Arizona mixed-conifer and ponderosa pine forest as a function of drought tolerance. Drought tolerance values followed Niinemets and Vallardes (2006), and ranged from 0 (no tolerance) to 5 (maximal tolerance). Species acronyms: ABCO = white fir, PIPO = ponderosa pine, POTR = quaking aspen, PSME = Douglas-fir, and QUGA = Gambel oak. Relative mortality was estimated as percent of live trees, with live tree density estimated under mortality scenario 2 (see text and Table 1 for details).

5. Discussion

Our results document extensive and accelerating mortality (Fig. 2) in southwestern mixed-conifer and ponderosa pine forests from 1997 to 2007. Observed tree mortality rates and cumulative tree mortality over this time period generally were high but not unprecedented relative to similar forest types (e.g., Savage, 1997; Maloney and Rizzo, 2002; Guarín and Taylor, 2005; Stephens and Gill, 2005; Breece et al., 2008). Estimates of mortality rate and cumulative mortality are difficult to compare between studies, however, as both are sensitive to factors such as length of time interval sampled and minimum tree diameter sampled.

The proximate cause for much of the observed mortality was damage due to a suite of forest insects. These included a complex of bark beetles (primarily *Ips* spp.) in ponderosa pine and pinyon pine (Negron et al., 2009; US Forest Service, 2009), Douglas-fir beetle (*Dendroctonus pseudotsugae*) and fir engraver (*Scolytus ventralis*) in Douglas-fir and white fir (US Forest Service, 2009), and western tent caterpillar (*Malacosoma californicum*) in aspen (Fairweather et al., 2007; US Forest Service, 2009). Although we did not quantify cause of death, signs of beetle activity such as pitch tubes and galleries were pervasive on dead and dying trees. Diseases and other forest insects likely played a secondary role in the observed mortality, especially in aspen (Fairweather et al., 2007; US Forest Service, 2009).

In most cases, however, insect and disease activity likely was mediated by long-term drought conditions in the study area (Breshears et al., 2005; Fairweather et al., 2007; Floyd et al., 2009; Negron et al., 2009; US Forest Service, 2009; see also Savage, 1997; Guarín and Taylor, 2005). This region has experienced a warm drought since 1996, with the period from 1996 to 2007 the driest 12-year period since 1950 (Hereford, 2007). Mean daily temperature in Flagstaff, AZ, increased by 2.3 °C from 1973 to 2007, annual precipitation was below average for 9 of 12 years from 1996 to 2007, winter precipitation, which is important hydrologically to local forests, was below average in 8 of 12 years (Hereford, 2007), and Weiss et al. (2009) documented unusually high levels of evapotranspirational demand in the southwestern USA during this time period. Presumably the hot, dry conditions stressed trees in these forests and rendered them more susceptible to insects and other pathogens (e.g., Breshears et al., 2005; Negron et al., 2009; see also

Guarín and Taylor, 2005; Mueller et al., 2005; van Mantgem et al., 2009; Allen et al., 2010).

Within this warm, dry period, the year 2002 represented a climatic extreme. A climate reconstruction from tree ring data suggested that 2002 was the third driest year in over 1400 years (Salzer and Kipfmüller, 2005), and both mean daily temperatures and maximum daily summer temperatures were above average during the summer of 2002 (Hereford, 2007). As a result, the Palmer drought-severity index (Alley, 1984) dropped to its most extreme value in the past 100 years (Koepke et al., 2010). Thus, this extremely warm, dry year, embedded within a long-term drought, immediately preceded the large spike observed in tree mortality. We do not know how much of the observed mortality from 2002 to 2007 occurred quickly in response to this extreme year, versus over longer time periods in response to cumulative stress from years of ongoing drought. Adams et al. (2009) demonstrated experimentally that warmer temperatures shortened the time to mortality in pinyon pine, however.

We expected that mortality would be greatest at lower elevation sites, which typically are warmer and drier than higher sites, and in high density stands, because high stand density typically increases moisture stress (Stone et al., 1999) and competition among trees and results in increased mortality (Savage, 1997; Allen and Breshears, 1998; Guarín and Taylor, 2005). Our data did not strongly support these hypotheses, however, as mortality was not significantly related to either elevation or stand density.

The latter finding is potentially important, because it may indicate that thinning high-density stands will not significantly reduce tree mortality in times of severe drought. Several other studies in the western U.S. also found no relationship between tree mortality and stand density in times of climatic stress, either across space (Floyd et al., 2009) or time (van Mantgem and Stephenson, 2007; van Mantgem et al., 2009), and Koepke et al. (2010) also found that parent material did not influence recent tree mortality in the ecotone between pinyon-juniper woodland and ponderosa pine forest. Presumably, the level of drought-induced mortality due to climate drivers in these studies was great enough to mask the effects of density-dependence that might have been apparent at lower mortality levels (Floyd et al., 2009; van Mantgem et al., 2009).

Failure to demonstrate a relationship between mortality and stand density may be an artifact of our sampling design, however. We sampled only trees ≥ 20 -cm dbh rather than all trees, and sampled trees on a 0.09-ha subplot within the larger (1 ha) snag plot. Consequently, we underestimated true stand density to an unknown extent, with that extent dependent on the relative contributions of trees < 20 cm dbh to overall stand density. Also, because stand density can vary across the landscape, the sampled subplot may not have been representative of density across the full plot. Thus, we remain uncertain about the strength of this result and suggest that this topic needs further investigation.

The observed patterns of species-specific mortality support the hypothesis that mortality was drought-mediated. Mortality rates were greatest in aspen and white fir, and proportion of live white fir was the strongest predictor of mortality rate in mixed-conifer forests. Aspen and white fir are the least drought-tolerant of the major tree species represented (Fig. 7), and may fall below a drought-tolerance threshold that renders them less able to tolerate recent conditions than the other major species present. White fir has increased greatly in many southwestern mixed-conifer forests since the advent of effective fire suppression efforts (Fulé et al., 2002, 2009). Thus, it could be argued that recent mortality will bring white fir densities back to levels more in line with its historical range of variability. The same argument could be made in

terms of overall tree density, which also has increased markedly in southwestern mixed-conifer forests (Fulé et al., 2002, 2009; Cocker et al., 2005). This argument cannot be made for aspen, however, which appears to be undergoing widespread decline in the western U. S. in response to drought and elevated temperatures (e.g., Fairweather et al., 2007; Worrall et al., 2008; Rehfeldt et al., 2009). Although aspen was more sensitive to assumptions regarding timing of mortality than other species analyzed here, it exhibited high relative mortality under all mortality scenarios evaluated. The high level of mortality observed in aspen suggests that it may be further reduced in density or extirpated in these forests in the future if these trends continue.

The relatively high mortality of large trees in our study as well as other studies (e.g., Mueller et al., 2005; Floyd et al., 2009; van Mantgem et al., 2009) suggests cause for concern, especially in mixed-conifer forest (Fig. 4). These larger trees are relatively rare on the landscape, but provide important habitat components for species such as the threatened Mexican spotted owl (Ganey and Dick, 1995). Additionally, large trees are relatively fire resistant and frequently are targeted for retention in forest restoration efforts (Allen et al., 2002; Stephens and Fulé, 2005; Kaufmann et al., 2007). Large proportional losses of these important habitat elements will hinder these restoration efforts.

6. Conclusions

Mixed-conifer and ponderosa pine forests in northern Arizona have experienced high and accelerating drought-mediated tree mortality between 1997 and 2007. This mortality is altering species composition and size-class distributions in these forests rapidly. These changes likely will have significant impacts on the native wildlife species inhabiting these forests, but those impacts are difficult to predict precisely.

The ultimate magnitude of ongoing changes likely will depend on climatic conditions interacting with disturbance regimes (e.g., McHugh et al., 2003; McKenzie et al., 2004; Parker et al., 2006; Breece et al., 2008). Most climate models predict increasing temperatures and aridity in the southwest (Seager et al., 2007). Our results suggest that these forests currently are not resilient to such changes. Consequently, management aimed at increasing resilience in these forests in the face of changing climate may be desirable (e.g., Millar et al., 2007). Possible approaches include treatments aimed at restoring more open stand conditions and appropriate species mixes in these forest types, which historically burned relatively frequently (Kaufmann et al., 2007; Fulé, 2008). Our data suggests that efforts to restore appropriate species mixes may be effective, as this will increase proportions of species with higher drought tolerance. Our data, as well as several other studies (e.g. van Mantgem and Stephenson, 2007; Floyd et al., 2009; van Mantgem et al., 2009), do not strongly support the hypothesis that stands with lower density experience lower mortality during severe drought, however. Thus, although reducing stand density should reduce competition for moisture and may increase resilience in most years, it is not clear that it will effectively reduce mortality during periods of severe drought. This is an area in need of further investigation, as thinning high-density stands is one of the more obvious management approaches to help alleviate moisture competition and tree mortality during drought periods.

Finally, spatial variability in mortality was pronounced, with some plots experiencing almost no mortality while others experienced extensive mortality. This is another important area in need of further investigation, as understanding patterns underlying that spatial variability may suggest other avenues for increasing resilience and conserving these forests in an era of changing climates.

Acknowledgments

We thank J. Jenness, G. Martinez, M. Stoddard, B. Strohmeier, R. White, and especially A. and J. Iníguez for their assistance in establishing plots, and L. Doll, D. and N. Ganey, and C. Vojta for assistance with plot sampling. For assistance with initial plot selection, we thank J. Ellenwood, B. Higgins, K. Menasco, C. Nelson, and G. Sheppard (Kaibab National Forest) and C. Beyerhelm, A. Brown, H. Green, T. Randall-Parker, C. Taylor, and M. Whitney (Coconino National Forest). Dave Turner provided advice on statistical analyses, and C.D. Allen, J. Kane, T.E. Kolb, P.J. van Mantgem and two anonymous reviewers reviewed earlier versions of this paper.

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