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To cite this article: Henry D Adams *et al* 2017 *Environ. Res. Lett.* **12** 115014

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Environmental Research Letters

OPEN ACCESS

RECEIVED
20 February 2017

REVISED
5 October 2017

ACCEPTED FOR PUBLICATION
16 October 2017

PUBLISHED
17 November 2017

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LETTER

Temperature response surfaces for mortality risk of tree species with future drought

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Keywords: drought, tree mortality, Pinus edulis, Pinus ponderosa, temperature, tree die-off, climate change ecology

Supplementary material for this article is available online

Abstract

Widespread, high levels of tree mortality, termed forest die-off, associated with drought and rising temperatures, are disrupting forests worldwide. Drought will likely become more frequent with climate change, but even without more frequent drought, higher temperatures can exacerbate tree water stress. The temperature sensitivity of drought-induced mortality of tree species has been evaluated experimentally for only single-step changes in temperature (ambient compared to ambient + increase) rather than as a response surface (multiple levels of temperature increase), which constrains our ability to relate changes in the driver with the biological response. Here we show that time-to-mortality during drought for seedlings of two western United States tree species, *Pinus edulis* (Engelm.) and *Pinus ponderosa* (Douglas ex C. Lawson), declined in continuous proportion with increasing temperature spanning a 7.7 °C increase. Although *P. edulis* outlived *P. ponderosa* at all temperatures, both species had similar relative declines in time-to-mortality as temperature increased (5.2% per °C for *P. edulis*; 5.8% per °C for *P. ponderosa*). When combined with the non-linear frequency distribution of drought duration—many more short droughts than long droughts—these findings point to a progressive increase in mortality events with global change due to warming alone and independent of additional changes in future drought frequency distributions. As such, dire future forest recruitment patterns are projected assuming the calculated 7–9 seedling mortality events per species by 2100 under business-as-usual warming occur, congruent with additional vulnerability predicted for adult trees from stressors like pathogens and pests. Our progressive projection for increased mortality events was driven primarily by the non-linear shape of the drought duration frequency distribution, a common climate feature of drought-affected regions. These results illustrate profound benefits for reducing emissions of carbon to the atmosphere from anthropogenic sources and slowing warming as rapidly as possible to maximize forest persistence.

Introduction

Plant mortality resulting from drought has been linked to the temperature dependence of ecophysiological and ecohydrological processes (Galiano *et al* 2010, Breshears *et al* 2013, Allen *et al* 2015), as noted in association with regional-scale die-off (Breshears *et al* 2005, Fensham *et al* 2009, Williams *et al* 2013).

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Drought, defined as a period of low precipitation, has caused elevated tree mortality events around the world (Allen *et al* 2010), many exacerbated by increased temperatures (Allen *et al* 2015). Trees under water stress are highly sensitive to elevated temperature because: (1) metabolic responses of biologically-active tissues scale with temperature and (2) atmospheric demand for water, i.e. vapor pressure deficit (VPD), increases with temperature, raising rates of evapotranspiration and reducing plant-available soil water (Breshears *et al* 2013, Williams *et al* 2013, McDowell and Allen 2015). These features interact, such that greater atmospheric demand associated with elevated VPD influences stomatal conductance and alters water-for-carbon trade-offs in plant function (Novick *et al* 2016). Experimental (Adams *et al* 2009, Will *et al* 2013, Duan *et al* 2014 2015) and observational (Breshears *et al* 2005) studies of drought have often found that increased temperature exacerbates the extent and rate of tree mortality (Allen *et al* 2015). Even in climates where drought has been uncommon, heat waves may result in tree mortality from water stress (Schär *et al* 2004, Matusick *et al* 2013, Teskey *et al* 2015, Bolte *et al* 2016, Colangelo *et al* 2017), although seasonality of temperature increase is important (Neumann *et al* 2017). In some regions where elevated tree mortality has been reported, drought and heat have also reduced surviving tree reproduction and regeneration, which could result in demographic shifts and vegetation change, including to non-forest ecosystems (Redmond *et al* 2012, Redmond and Barger 2013, Redmond *et al* 2015).

Despite the critical linkage between temperature and plant mortality, increased temperature effects on how long tree species can survive during drought have only been studied experimentally for no more than a single-step temperature increase. Consequently, the nature of mortality responses for any tree species across a range of elevated temperatures—the shape of response surface—remains unknown and is not factored into projections for tree species, regardless of life stage. While research into the physiological causes of tree mortality in response to drought offers the potential for future development of mechanistic models (Anderegg *et al* 2015, McDowell *et al* 2016), empirical relationships between tree death and climate can provide rapid initial assessments of forest vulnerability (Adams *et al* 2013). We assessed the temperature sensitivity of time-to-mortality during experimental drought across a 7.7 °C range of temperatures for seedlings of two widespread North American pine species, *P. edulis* (piñon pine) and *P. ponderosa* (ponderosa pine). We hypothesized that (1) increased temperatures would result in earlier seedling mortality from drought for both species, and (2) species differences in drought tolerance would lead to earlier mortality for *P. ponderosa* than *P. edulis*. We based our first hypothesis on the findings of several drought-induced mortality experiments with single-step temperature treatments that earlier mortality was observed under higher temperatures for small trees of *P. edulis* (Adams *et al* 2009), and seedlings of *Eucalyptus radiata* (Duan *et al* 2014), *Pinus radiata* (Duan *et al* 2015), and ten tree species from the south-central US (Will *et al* 2013). We based our second hypothesis on past findings that *P. edulis* is less vulnerable to xylem embolism from drought (Martínez-Vilalta *et al* 2004), has a lower sensitivity of radial growth to drought (Adams and Kolb 2005), occurs at drier sites, and experienced less drought-induced mortality at sites where the species co-occur, than *P. ponderosa* (Koepke *et al* 2010). Based on the experimentally quantified temperature sensitivity of time-to-mortality, we conducted a simple projection to assess how higher temperatures would increase the likelihood of future mortality events from drought given a quantified drought frequency distribution function, where shorter droughts occur more frequently than longer droughts. We tested our hypotheses experimentally on seedlings and place these results in the context of expectations for stressors that increase the probability of mortality in adult trees associated with drought, higher temperature, pathogens, and pests.

Methods

Mortality experiment

We obtained pine seedlings in 'cone-tainers' (height 21 cm, volume: 175 ml) of two species (*P. edulis* and *P. ponderosa*) from the Colorado State Forest Service Nursery (Fort Collins, CO) in March 2010. The nursery used a Colorado seed source for *P. ponderosa*, but for *P. edulis*, seeds were obtained commercially, and their provenance is unknown. Seedlings were kept in growth chambers (Conviron, Winnipeg, Manitoba, Canada) at 25 °C during the day under photosynthetically active radiation of ~700 μmol m^{-2}sec^{-1} and at 10 °C at night. We transplanted seedlings into tree pots (height: 36 cm, volume: 2.8 l, Stuewe and Sons, Tangent, OR) in September 2010 with potting soil (Sunshine Mix #4, Sungrow Horticulture, Bellevue, WA).

We conducted two drought experiments with seedlings in the growth chambers to test our hypotheses. For both experiments we based variability in diurnal temperatures on data from a meteorological station located at a piñon-juniper woodland near Valle, Arizona, using average daily maximum and minimum temperatures from July 2009 and 2010. To adjust diurnal temperatures to the higher elevation, cooler conditions of the piñon–juniper woodland/ponderosa pine forest ecotone, we used the difference in monthly maximum and minimum temperature between the station data and the mean of 20 years of interpolated July PRISM data (www.prism.oregonstate.edu, PRISM group, Corvallis, OR) for a point at the ecotone near the station, a reduction of ~2.4 °C. This resulted in an ambient treatment of 25/11 °C day/night. In the first experiment, we excluded water

from seven randomly selected seedlings of each species, under each of four temperature treatments: (1) ambient (25/11 °C day/night), (2) +3.6, (3) +5.9, and (4) +7.7 °C above ambient. For the second experiment we excluded water from four randomly selected seedlings of each species, under (1) ambient temperature, (2) +4.4, and (3) +7.7 °C. These treatments were chosen to simulate the range of temperatures projected for the southwest US by 2100 under a business-as-usual climate scenario (figure S1, available at stacks.iop.org/ERL/12/115014/mmedia). For both experiments, following an initial watering to saturation, we completely withheld water from seedlings for the duration of the drought treatment. Seedling foliage color was noted three times per week, and seedlings were declared dead when we observed 90% foliar browning (Adams *et al* 2009). Foliar browning typically took 1−2 weeks from initiation before reaching the 90% threshold. The first experiment started in April 2011 and the second in October of 2011, and both experiments continued until all seedlings in the water exclusion treatments died. Survival data were inadvertently lost for two *P. ponderosa* seedlings from the first experiment, one each in the ambient and +3.6 °C treatments, and one *P. edulis* seedling from the second experiment in the ambient treatment, reducing sample size in these treatments.

Data analysis

We analyzed the relationship between time-to-mortality with temperature using ordinary least squares linear regression in SPSS Statistics 22 (IBM Corporation, Armonk, NY). Time-to-mortality data were pooled from both experiments for analysis, as results were not significantly different for the ambient and +7.7 °C treatments between experiments ($p > 0.05$). We calculated relative percent change in time-to-mortality with temperature increase and analyzed this with linear regression for both species. We used the Wald test for common slope to compare regression slope results between *P. edulis* and *P. ponderosa*, and also between *P. edulis* seedlings and small *P. edulis* trees using data from a similar drought and temperature mortality experiment (Adams *et al* 2009) with SMATR 2.0 (Falster *et al* 2006). To further compare our experimental results to results of previously published studies we calculated a mean reduction in time-to-mortality per unit increase in °C, from results reported in the literature for *P. edulis* (Adams *et al* 2009), *E. radiata* (Duan *et al* 2014), *P. radiata* (Duan *et al* 2015), and ten central USA tree species (Will *et al* 2013).

To assess the implications of our experimental results for future seedling die-off in the southwest US with climate change, we calculated a simple projection based on the historic frequency distribution of drought duration for the lower forest boundary ecotone (Adams *et al* 2009, Allen *et al* 2015). We used precipitation data from four climate stations in the southwest US located near the lower forest boundary ecotone (Western Regional Climate Center, www.wrcc.dri.edu: Blanding, UT, Cimarron, NM, Durango, CO, Williams, AZ) to calculate a historical frequency distribution of drought duration. We calculated the mean of precipitation totals at each of the four stations for our regional record of precipitation. We defined drought in this record as the number of consecutive months that had less than the mean monthly precipitation for each month during the 107 year record (Adams *et al* 2009). We avoided months with excessive missing data late in the historical record, and used the period for which data were available for all four stations, 1905−2011, resulting in a 107 year frequency distribution.

We identified the 2002/2003 drought as a period known to have caused widespread regional seedling mortality (Breshears *et al* 2005), which then can be used as a baseline for our predictions (droughts longer than the baseline induce mortality, whereas droughts shorter than the baseline will not without an increase in temperature). This drought caused widespread mortality of seedlings and trees for many species, including *P. edulis* and *P. ponderosa*, across the southwest US (Breshears *et al* 2005, Shaw *et al* 2005, Allen *et al* 2010, Koepke *et al* 2010). *P. edulis* mortality was higher for adult trees (> 10 cm basal diameter) than seedlings and saplings (Mueller *et al* 2005). For *P. ponderosa*, whether seedlings or adults had higher mortality varied across sites (Gitlin *et al* 2006). For other long droughts in our record (1910, 1945/1946, 1956), regional observations of tree response, including potential mortality, were lacking.

In our calculated drought record the 2002/2003 drought lasted 9 months regionally, which we used as our ambient baseline. We then calculated the duration of regional drought that could cause mortality for +4, +5.9, and +7.7 °C above ambient conditions using the linear relationship between relative percent change in time-to-mortality and temperature for both species. We fit an exponential function to the frequency distribution of drought duration (SPSS Statistics 22) to calculate the frequency of these shorter droughts that could cause seedling mortality with increased temperatures. From these calculations we projected the additional number of drought events that would cause widespread mortality under the temperature increases that would cause an 8, 7, 6, and 5 month drought to become lethal for each species. The effect of several assumptions in these methods on our projections was assessed with sensitivity analyses (see the supplementary information). We also calculated the cumulative number of additional mortality events for both species anticipated up to the year 2100 using our projections under two emissions scenarios, RCP 2.6 and RCP 8.5. For this calculation, we used a 21 model ensemble mean surface air temperature for the four corners region of the southwest US available from the Coupled Model Intercomparison Project Phase 5 (CMIP5; http://cmip-pcmdi.llnl.gov/cmip5/; figure S1). Note

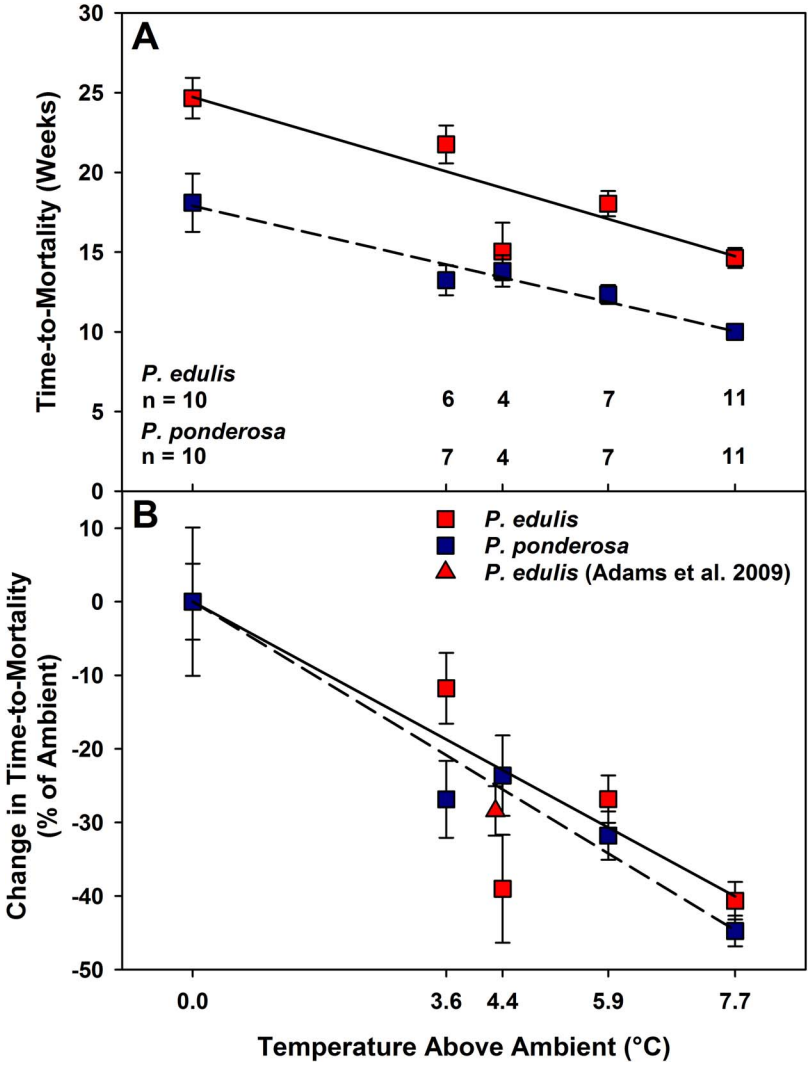

Figure 1. Time-to-mortality in weeks (*a*) and as a percent change from ambient (*b*) during drought for seedlings of two pine species, *P. edulis* and *P. ponderosa*, across a range of temperatures. Linear regressions calculated from individual seedling data for *P. edulis* (solid) and *P. ponderosa* (dashed) are shown and sample size (n) is indicated at each temperature treatment for each species in (*a*). Linear regressions were also calculated for relative change in time-to-mortality for each species with the intercept forced through the origin (0, 0) in (*b*). Percent change from ambient in time-to-mortality is also shown in B for a previous experiment with reproductively mature trees of *P. edulis* (Adams *et al* 2009). Error bars are standard errors (SE).

that these calculations assume regional drought has a similar relative effect of water stress across the ranges of *P. edulis* and *P. ponderosa* that scales with differences in species drought tolerance.

Results

We found that time-to-mortality for both *P. edulis* and *P. ponderosa* seedlings was highly sensitive to elevated temperature during experimental drought, and declined linearly in continuous proportion with increasing temperature ($p < 0.001$, figure 1(*a*)). Across all temperature treatments, *P. edulis* seedlings persisted longer than *P. ponderosa* seedlings during the drought (figure 1(*a*)). However, the relative reduction in time-to-mortality for *P. edulis* and *P. ponderosa* of 5.2 (SE 0.324) and 5.8 %/°C (SE 0.247) were similar, i.e. there was no difference between species in the slope of relative change in time-to-mortality with temperature ($p > 0.05$, figure 1(*b*)). For *P. edulis* this result was not significantly different than the 6.5%/°C observed in a previous experiment for small trees of the same species with a 4.3 °C single-step temperature increase ($p > 0.05$; figure 1(*b*); Adams *et al* 2009).

Since elevated temperatures reduced time-to-mortality, future temperature increases expected with global change should reduce the duration of drought needed to cause widespread mortality (Adams *et al* 2009, Allen *et al* 2015), which we assessed with a die-off frequency projection. The 2002/2003 drought associated with a widespread tree mortality event impacting seedling through adult life stages (Breshears *et al* 2005, Mueller *et al* 2005, Gitlin *et al* 2006, Redmond *et al* 2015) lasted 9 months in our regional drought record. Applying our reduction in time-to-mortality with increasing temperature to this 9 month baseline,

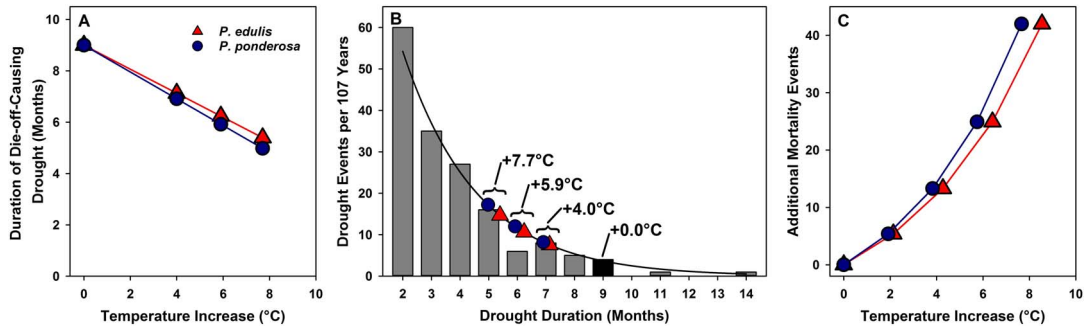

Figure 2. The implications of reduced time-to-mortality with increased temperature for regional tree die-off. The duration of regional drought sufficient to cause widespread tree die-off with increasing temperature, as calculated from the relative change in time-to-mortality figure 1(*b*) for the 2002/2003 drought known to have caused widespread mortality in both *P. edulis* and *P. ponderosa* (*a*). This calculation uses the 2002/2003 drought as a baseline, and this drought was 9 months in duration in our regional record (see also figure S2). The regional drought duration frequency distribution for the lower forest boundary in the southwest US is shown over 107 years (gray bars, (*b*)). The 9 month 2002/2003 drought (+0 °C) is indicated with a black bar. An exponential curve fitted to the frequency distribution is shown (R^2=0.96, $p > 0.001$), and the shift in duration of die-off causing drought with increased temperature is projected for *P. edulis* (red triangles) and *P. ponderosa* (blue circles) using experimental results at three temperatures (+4, +5.9. +7.7 °C). The additional number of mortality events per century projected from increased temperature are shown as droughts of 9, 8, 7, 6, and 5 months duration (shown as points) become sufficient to cause tree mortality with increasing temperature (*c*).

temperature increases of 4.0, 5.9, and 7.7 °C indicated that shorter droughts than the baseline, of ~7, ~6, and ~5 months, respectively, would become sufficient to cause widespread seedling mortality in both pine species across their ranges (figure 2(*a*)). Individually, the droughts that would become lethal at each of our three experimental temperature increases (+4, ~+6, and ~+8 °C) occurred 7.5, 10.6, and 14.7 times per century for *P. edulis* and 8.2, 12.0, and 17.2 times per century for *P. ponderosa* in the historical record (figure 2(*b*)). Cumulative calculations from these values result in a progressive increase of 5, 13, 24, and 41 additional mortality events per century as shorter droughts of 8, 7, 6, and 5 months in duration become sufficient to cause widespread seedling mortality (figure 2(*c*)). This progressive increase mainly arises from the characteristics of the historically-derived drought duration frequency distribution, where shorter droughts are much more common than longer droughts (figure 2(*b*)) (Adams *et al* 2009, Lauenroth and Bradford 2009, Allen *et al* 2015). We next considered the effect of temperature sensitivity (figure 2(*c*)) on the risk of mortality events as temperatures increase over the next century under two scenarios, high emissions (RCP 8.5; 'business as usual') and extensive emissions mitigation (RCP 2.6), using model ensemble temperature predictions for the southwest US (figure S1). Under the RCP 2.6 scenario, temperature increases only ~1 °C across the region and the cumulative increase in additional mortality events by 2100 was limited (~1.5 for *P. edulis*, ~1.8 for *P. ponderosa*; figure 3). Under the RCP 8.5 scenario, a ~5.4 °C temperature increase leads to the risk of ~7.2 additional seedling mortality events for *P. edulis* and ~8.5 for *P. ponderosa* by 2100 (figure 3).

Discussion

We found that drought-induced mortality of tree species was sensitive to a range of temperatures. The response surface in time-to-morality was a constant proportion of the change in temperature above ambient. Our finding of reduced time-to-mortality for *P. edulis* and *P. ponderosa* by 5.2% and 5.8% per 1.0 °C increase across a 7.7 °C range in temperature is consistent with results reported for prior seedling experiments with single-step-temperature-changes. In addition to the earlier experiment with small *P. edulis* trees (Adams *et al* 2009), similar relative declines in survival time have been reported for seedlings of *Eucalyptus radiata* (Duan *et al* 2014), *Pinus radiata* (Duan *et al* 2015), and ten tree species from the south-central US forest/grassland ecotone (Will *et al* 2013). On average, these studies found a ~4.7% reduction in time-to-mortality for every 1 °C increase in temperature. We also observed that *P. edulis* survived longer than *P. ponderosa* at all temperatures (figure 1), a result consistent with differences between these species in ecological patterns and physiology of these co-occurring species. *P. edulis* is more drought tolerant than *P. ponderosa*, as *P. edulis* can maintain stomatal conductance and xylem hydraulic conductivity at lower water potentials (Kolb and Stone 2000, Martínez-Vilalta *et al* 2004, Garcia-Forner *et al* 2016), and has less growth sensitivity to drought where the species co-occur than *P. ponderosa* (Adams and Kolb 2005). Our seedling-specific results are also consistent with patterns of adult demography: *P. edulis*, which occupies drier habitat than *P. ponderosa* (Koepke *et al* 2010, Adams and Kolb 2005), also had lower tree mortality at the lower forest boundary than *P. ponderosa* during the 1950s' drought in northern

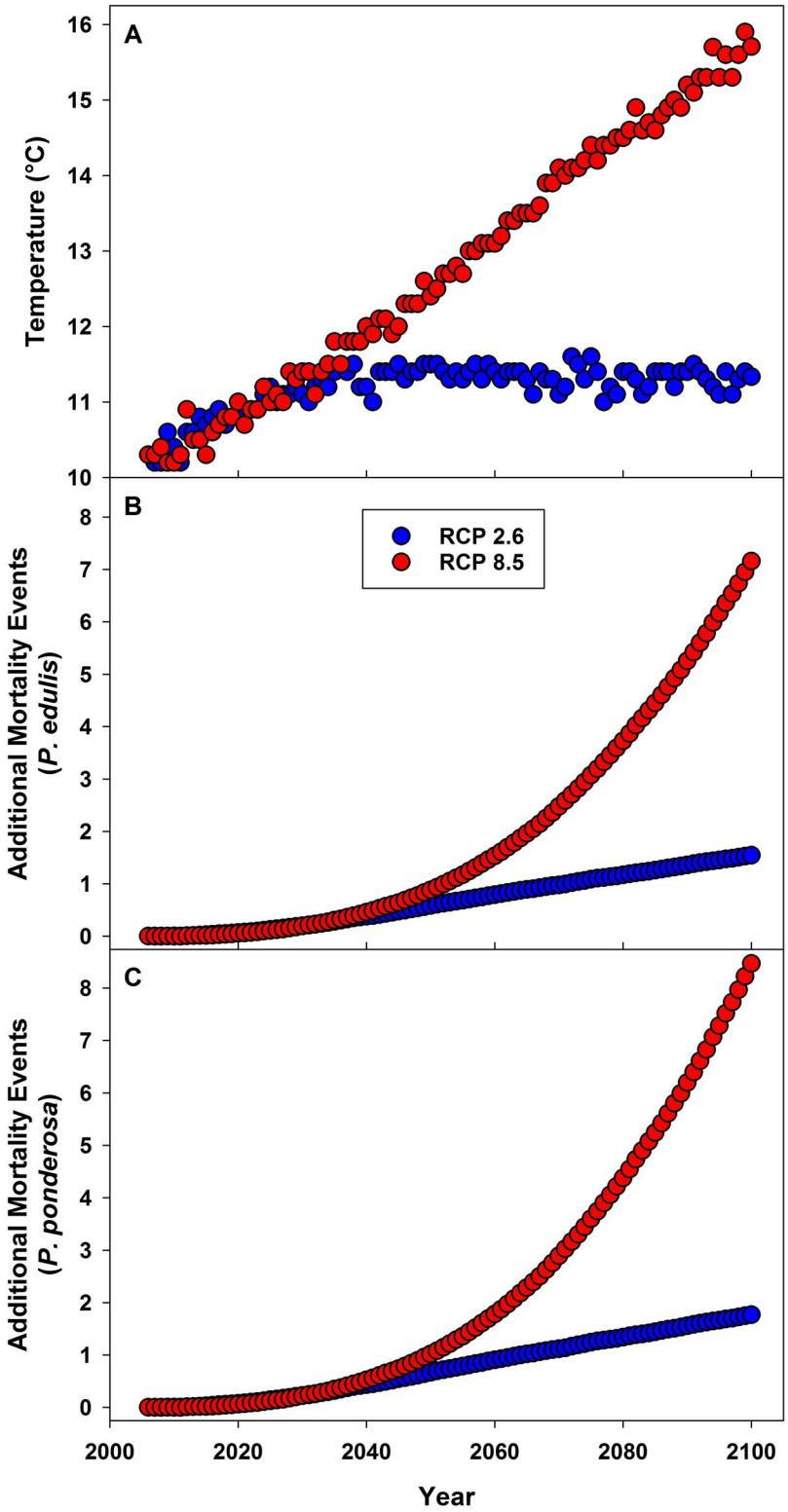

Figure 3. Projection of additional tree mortality events in response to projected CMIP5 ensemble mean temperatures for the 'Four Corners' region of the southwest United States (figure S1) based on the relationships between temperature increase and additional mortality events shown in figure 2(*c*). Mean annual temperature (*a*) and die-off (*b*) and (*c*) projections are shown for both RCP 2.6 and 8.5 scenarios. The cumulative sums of additional mortality events are shown separately for *P. edulis* (*b*) and *P. ponderosa* (*c*).

New Mexico (Allen and Breshears 1998). Although our results for *P. edulis* and *P. ponderosa* were consistent with autecological differences between species, we did not explore provenance and genetic differences within species, which can affect tolerance of drought and high temperatures (Matyas 1994, Sthultz *et al* 2009, Zang *et al* 2014), and influence seedling survival (Bolte *et al* 2016).

Although we observed a linear reduction in time-to-mortality from drought with increasing

temperature, the historic trend in the frequency of drought duration formed an exponential distribution (Adams *et al* 2009, Allen *et al* 2015). Therefore, our projections based on this drought duration frequency distribution revealed that lethal drought could become much more frequent with increased temperature—a non-linear response caused primarily by the shape of this frequency distribution. This progressive effect of increasing temperature on the future risk of lethal events was readily apparent whether we consider a constant elevated temperature in the future (figure 2(*c*)), or a realistic increase in temperature based on IPCC scenarios for climate change (figure 3). Notably, this non-linear response did not disappear in our sensitivity analysis of assumptions used in these projections (figure S2), because the drought duration frequency distribution retained its exponential shape (figure S3). So even if time-to-mortality during drought for seedlings in the field is only half as temperature-sensitive as we measured in our experiment, we can still expect a progressive increase in additional mortality events (figures S2(*a*) and (*d*)).

We emphasize that the exponential form of the drought duration frequency distribution—that shorter droughts are much more frequent than longer droughts—is not a climate phenomenon limited to the southwest US, but is common for drought-affected regions globally (Dalezios *et al* 2000, AghaKouchak *et al* 2014, Trenberth *et al* 2014). Therefore, increased drought-induced seedling mortality with higher temperatures should be expected in any region where survival during drought is sensitive to temperature—a response consistently observed in tree seedlings and saplings for which this has been tested (Adams *et al* 2009, Will *et al* 2013, Duan *et al* 2014, 2015). Moreover, our projections are conservatively based on the historical drought frequency distribution. For many regions, including the southwest US, the variability in future precipitation is expected to increase with climate change, causing an increase in drought frequency (Overpeck and Udall 2010, IPCC 2013) that would result in additional mortality events over our calculations. Although precipitation projections with global change are often uncertain, projections of temperature change have a much higher degree of confidence (IPCC 2013, Cañon *et al* 2011). Our results demonstrate how large changes in ecological disturbance from drought can be anticipated from temperature change alone, even if the amount and distribution of precipitation is uncertain or unchanged in the future (Trenberth *et al* 2014, Mazdiyasni and AghaKouchak 2015, McDowell *et al* 2016).

Our experimental and projection results are specific to seedlings but we expect these have implications for other life stages, including adults. Although seedling studies have been recognized as an effective method of investigation in tree mortality prediction where breakthrough tests are needed (McDowell *et al* 2013), caution should be used in extrapolating from our growth chamber experiments to large adults in the field (Leuzinger *et al* 2009). However, despite a lack of logistically challenging temperature-manipulation experiments in the field (McDowell *et al* 2013), the sensitivity of mature trees to temperature during drought is well-documented (Adams and Kolb 2005, Breshears *et al* 2005, Clifford *et al* 2013, Williams *et al* 2013, Adams *et al* 2015, Allen *et al* 2015, Bennett *et al* 2015, McDowell and Allen 2015). Differences among mature trees, juvenile trees, and seedlings in their degree of drought sensitivity, and temperature sensitivity during drought, are likely. Seedlings have shallower rooting depths (Christina *et al* 2011), lower internal water stores (capacitance, Scholz *et al* 2011), and lower carbohydrate storage relative to mature trees (Sala *et al* 2012), which should make seedlings more vulnerable to drought (McDowell *et al* 2013). However, large trees have greater demands for water than seedlings, and have often maximized their exploration of soil water resources, such that the root-to-shoot ratio of seedlings is often higher (Ryan *et al* 2006, McDowell *et al* 2013). Moreover, large trees are often more vulnerable to biotic attack than seedlings (Axelson *et al* 2010). Following drought in the late 1990s and early 2000s in northern Arizona, mortality rates for both *P. edulis* and *P. ponderosa*, increased with tree size, likely a result of bark beetle preference for larger trees (Mueller *et al* 2005, Gitlin *et al* 2006). Our experimental results for *P. edulis* seedlings were consistent with the response of small (reproductively mature) trees of the same species in a similar experiment (figure 1(*b*); Adams *et al* 2009). However, if seedlings are more sensitive to drought, and to temperature increase during drought, than adults, we expect fewer mortality events for adult trees than we have specifically projected for seedlings. Such an effect is evident in our assessment of projection assumptions, where reduced sensitivity lowers the number of additional mortality events, but relationships remain non-linear (figure S2). Given that adult trees are drought- and temperature-sensitive, we expect that the shape of the projected relationship—a progressive increase in mortality events with increasing temperature—would not be different for adults, as this non-linearity derives from the intrinsic nature of the frequency distribution for drought duration, not the degree of temperature sensitivity (figure 2(*b*), figure S2).

Our projections of a pronounced increase in seedling mortality under higher temperatures were consistent with the overall tree species mortality projections of several other studies that used different approaches. A thousand-year index of forest drought stress for the southwest US, calculated from tree-ring growth records and their relationship with warm season VPD and cool-season precipitation, was positively correlated with recent tree mortality rates (Williams *et al* 2013). Forecasting this index into the future under a business-as-usual climate scenario (~+5 °C temperature increase, slight precipitation decrease) produced

a projection that mean conditions from 2050 through 2100 will be equivalent to, or more stressful than, the most extreme droughts of the past 700 years, which caused extensive regional tree mortality (Swetnam and Betancourt 1998, Williams *et al* 2013). In comparison to a future when climate conditions are conducive to annual occurrence of widespread tree mortality events, our projection at +5 °C of 17–20 additional mortality events per century appears fairly conservative. Our projection of 7.2–8.5 mortality events over the next century under the RCP 8.5 scenario, which is demographically unsustainable for the persistence of these slow-growing semiarid woodlands and forests, was also consistent with analogous predictions of conifer mortality in the southwest US from the ED(X) model parameterized to the physiological responses of mature *P. edulis* and *Juniperus osteosperma* to experimental drought (McDowell *et al* 2016). It should be noted that successful reproduction and tree establishment events in these forest communities are already infrequent, and could become more so in the future because drought and increased temperature also reduce reproduction and recruitment (Redmond *et al* 2012, Redmond and Barger 2013). Without regeneration, this increased seedling and tree mortality would shift drier forests to savanna or grassland ecosystems (Neilson *et al* 1992, McDowell and Allen 2015, Redmond *et al* 2015).

Conclusion

Tree mortality alters ecological interactions among species, affecting plant community composition, wildlife habitat, and biogeochemical cycles (Anderegg *et al* 2013). Forests also exert strong effects on earth system processes though their influence on the terrestrial carbon sink, land surface energy balance, and hydrological cycling (Bonan 2008, Anderegg *et al* 2013), not only locally where forest die-off occurs but also elsewhere via ecoclimate teleconnections (Garcia *et al* 2016, Stark *et al* 2016). However, the magnitude of these effects depends on the potential for ecosystem recovery, determined by whether seedling regeneration and recruitment follows mortality (Adams *et al* 2012, Schwalm *et al* 2017). Our results reveal that time-to-mortality during drought for seedlings of two western United States tree species, *Pinus edulis* (Engelm.) and *Pinus ponderosa* (Douglas ex C. Lawson), declined proportionally with increasing temperature across four experimental treatments spanning a 7.7 °C increase. The progressive increase in widespread seedling mortality we predict as temperatures rise is a potential positive feedback on global climate change, as limited recruitment in dying forests lowers potential terrestrial C uptake. The potential relevance of our seedling results—that the nature of the temperature sensitivity for drought-induced mortality is linear—to trees of other life stages would, if applicable, have important implications for empirical prediction of drought-induced tree mortality and its earth system feedbacks into global change models (Adams *et al* 2013, Allen *et al* 2015, Huang *et al* 2015, McDowell and Allen 2015). That tree mortality can be expected to accelerate across a range of increased temperatures should be represented in such models and motivate policy to reduce the anthropogenic drivers of climate warming. As continued temperature increases will progressively cause more tree mortality, these results clearly illustrate the profound benefits of slowing warming as rapidly as possible, as forest persistence is critical for globally coordinated carbon management.

Acknowledgments

This research was supported by, Biosphere 2, though the Philecology Foundation (Fort Worth, TX), the Los Alamos National Laboratory and Pacific Northwest National Laboratory LDRD programs, US DOE Biological and Environmental Research, NSF Macrosystems Biology (EF-1340624, EF-1550756), NSF Critical Zone Observatories (EAR-1331408), the Arizona Agriculture Experiment Station, and the Oklahoma State University College of Arts and Sciences. This research was developed under STAR Fellowship Assistance Agreement no. FP-91717801-0 awarded by the US Environmental Protection Agency (EPA). It has not been formally reviewed by EPA. The views expressed in this publication are solely those of the authors, and EPA does not endorse any products or commercial services mentioned in this publication. We thank Paula Arias and Juan Villegas for assistance with CMIP5 data, and three anonymous reviewers for providing feedback on the manuscript.

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