Title: Rapid and surprising dieback of Utah juniper in the southwestern USA due to acute drought stress

Steven A. Kannenberg[1*], Avery W. Driscoll[1], Danielle Malesky[2], William R.L. Anderegg[1]

[1]School of Biological Sciences, University of Utah, Salt Lake City, UT

[2]Forest Health Protection Region 1, U.S. Forest Service, Coeur d’ Alene, ID

*corresponding author

Abstract

For nearly two decades, the American southwest has been in the grips of a long-term ‘megadrought’, punctuated by a number of short and severe ‘global change type droughts’ (i.e., negative precipitation anomalies co-occurring with high temperature). These events have caused widespread mortality of the drought-sensitive piñon pine (*Pinus edulis*) while co-dominant *Juniperus* spp. have historically been much more drought tolerant and thus have rarely died. However, a severe drought occurred in 2018 that rapidly (<1 year) caused canopy dieback of *Juniperus osteosperma* across a vast area of southeastern Utah. In order to uncover the etiology behind this surprising canopy dieback event, we set up a series of survey plots that captured gradients in microclimate, topography, and canopy dieback severity. We also quantified xylem hydraulic damage and biotic agents associated with tree mortality, in declining junipers to identify the primary cause of juniper canopy dieback. We observed that juniper canopy dieback was most severe (>60% canopy dieback) at hot, dry, low elevation sites, and was associated with drought-induced hydraulic damage. There was no evidence suggesting biotic agents were the primary drivers of this canopy dieback event, implicating the acute effects of drought as the main causal agent. The speed and scale of this drought-induced juniper canopy dieback

seems to be historically unprecedented in the region and foreshadows an uncertain future for piñon-juniper woodlands as the region continues to get warmer and drier.

Introduction

Drylands cover over 40% of the Earth's land surface and are home to nearly 40% of the global population, yet are rapidly degrading (Reynolds et al., 2007). Climate change is also stressing these ecosystems due to aridification coupled with an increase in the frequency and severity of drought (Bradford et al., 2020; Dai, 2013; Giorgi et al., 2011). These ongoing changes could lead many dryland species to tipping points beyond which they cannot recover (Bestelmeyer et al., 2015; Hoover et al., 2020).

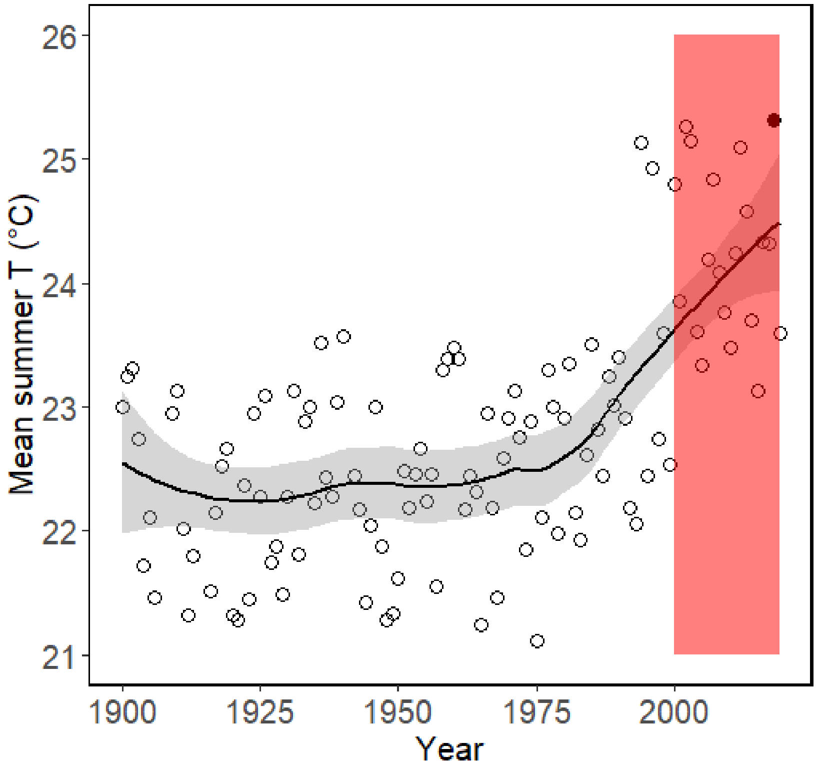
Emerging evidence indicates that piñon-juniper woodlands, the most widespread forest type in the American southwest (Shaw et al., 2005), may be approaching one of these critical stages due to a multi-decadal 'megadrought' that has been ongoing since 2000 (Cook et al., 2015; Williams et al., 2020). In the region, the past 19 years have been the second driest period in the last 1200 years, the severity of which has been significantly exacerbated by anthropogenic warming (Williams et al., 2020). The onset of this megadrought coincided with two 'global change type droughts' in 1996 (Ogle et al., 2000) and 2002-2003 (Shaw et al., 2005), in which the stress of low precipitation was exacerbated by anomalously high temperatures (Breshears et al., 2005). These droughts, in combination with outbreaks of piñon ips (*Ips confusus*) beetles (Clifford et al., 2008; Gaylord et al., 2015; Meddens et al., 2015), caused widespread dieback of *Pinus edulis* (hereafter referred to as piñon) that exceeded 40% of basal area in some stands (Breshears et al., 2005; Clifford et al., 2011; Ogle et al., 2000).

A rich history of research into the eco-physiology and ecology of piñon-juniper woodlands indicates that piñons are generally more drought sensitive, while the primary co-dominant species, *Juniperus* spp., tends to be more drought tolerant due to a combination of xylem that are more resistant to hydraulic damage (Koepke and Kolb, 2013; Linton et al., 1998; West et al., 2007b), a highly sectorial hydraulic architecture (Schenk et al., 2008), deeper roots (Schwinning et al., 2020), and lesser reliance on summer precipitation (West et al., 2007a). Indeed, this dynamic has been observed during nearly every drought in this region in the past several decades, where juniper species were generally able to survive following drought while piñons have died due to a combination of drought stress and biotic attack from the piñon ips beetle. To our knowledge, only one study has documented severe drought-induced dieback of *Juniperus* spp. (up to 65% canopy death) in the American southwest (Bowker et al., 2012), but dieback in this case was limited in spatial scale to a *ca.* 0.015 km^2 stand.

Another severe drought occurred in the Four Corners region (the confluence of Colorado, Utah, Arizona, and New Mexico) in 2018, localized in San Juan County in southeastern Utah (Fig. 1). This drought was likely one of the most severe single-year droughts in the historical record. The water year of 2018 (October 2017 to September 2018) had the lowest amount of precipitation and the highest mean vapor pressure deficit (VPD) of any individual year in the last 40 years (data from TerraClimate, Abatzoglou et al., 2018), and the region was in a category D4 ‘exceptional drought’ (the highest level attainable) for 38 consecutive weeks according to the U.S Drought Monitor. However, counter to past droughts in the region, the 2018 drought has caused widespread dieback of Utah juniper (*Juniperus osteosperma*, hereafter referred to as juniper). This dieback began only months after the cessation of the drought, a striking observation considering multiple years of experimentally-induced drought have previously been necessary to cause dieback in this species (Gaylord et al. 2013). Signs of dieback were detected in 2019 using remote sensing methods across 39% of San Juan County (Campbell et al., 2020), with severe dieback (>50% canopy dieback) localized in spatially heterogeneous ‘hotpots’. However, besides its occurrence, severity, and spatial scope, nothing is yet known about the proximal mechanisms contributing to the dieback of a traditionally highly drought tolerant species, nor is it known how this severe canopy dieback is linked to whole tree mortality.

Here, we document the etiology of this recent juniper dieback and attempt to identify its topographic, climatic, eco-physiological, and biotic drivers. This unique tree dieback event runs counter to current paradigms of piñon-juniper drought responses and thus an understanding of this event is urgently needed to forecast the fate of piñon-juniper woodlands.

Fig. 1. Mean summer temperature (June – August) over time at our lowest elevation site. The black line indicates a smoothed loess curve with a span of 0.5 while the gray shading indicated the 95% confidence interval for the smoothed line. The 'megadrought' period (2000 – 2019) is highlighted in red, while the black point represents the drought year of 2018.



Methods

Site selection

Initial observations of juniper dieback in 2018 were found to be concentrated in hotspots across San Juan County, UT. In May 2019, a series of twelve 15 m radius plots were set up across a *ca.* 100 km gradient that encompassed variation in juniper dieback, elevation, and microclimate (Fig. 2). All sites were selected to be generally flat so as to avoid variation in slope and aspect. Within each of these plots, five mature juniper trees that were representative of plot-level variation in dieback were tagged for targeted monitoring and eco-physiological measurements (described below, hereafter referred to as "focal trees").

Stand surveys

In May 2019 and October 2019, stand surveys were conducted at these plots that generally followed U.S. Forest Service Forest Inventory and Analysis (FIA) protocols. Briefly, all trees larger than 2.5 cm diameter at root collar (DRC) were measured for DRC (182 piñons and 396 junipers total). In order to account for the common occurrence of juniper trees with multiple stems, we added DRC for all stems within a 0.3 m radius of the largest stem, as long at those stems were angled towards the main stem. For each tree, species was noted, and two observers used the foliage color to estimate the percent of all leaves that recently died, with the greenest foliage as a reference point. These two estimates were averaged together to obtain a mean canopy dieback percent for each tree. The estimates between the observers were highly consistent (slope = 0.99, r^2 = 0.97). Both juniper and piñon tend to drop their dead foliage within two years, and recently dead foliage is distinctly reddish-brown. Thus, estimates of canopy dieback are likely strongly indicative of dieback following the 2018 drought.

We also noted the presence or absence of juniper mistletoe (*Phoradendron juniperum*) on each measured tree during these stand surveys.

Hydraulic and leaf water potential measurements

In May and July 2019, all 60 focal trees were measured for predawn (2 – 5 am) and mid-day (12 – 3 pm) leaf water potentials using a Model 610 Scholander-type pressure chamber (PMS Instruments, Corvallis, OR). During July 2019, samples were also collected to measure various aspects of xylem hydraulics. For these analyses, one branch (20 – 50 cm) per focal tree was chosen for sampling so as to represent whole-tree canopy dieback (i.e., branches with 50% foliage dieback were sampled on a tree with 50% total canopy dieback). The cut end of these branches was wrapped in wet paper towers, put on ice, and transported to the laboratory where they were kept in a cold room until they were analyzed within one week. Prior to analysis, both ends of the samples were re-cut under water to a length of 5 – 10 cm (with no branching) and branch diameter was measured.

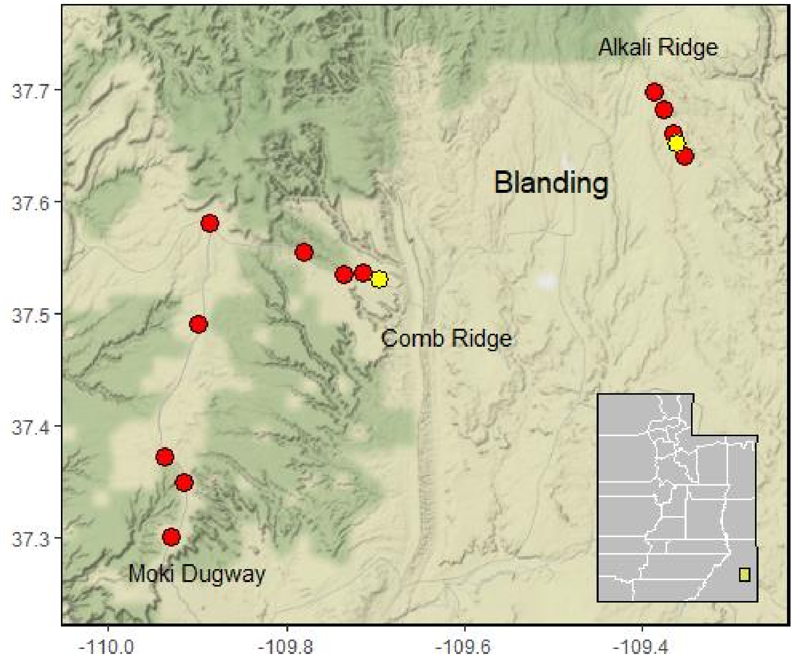
Hydraulic conductance (K_h) was measured via a pressure-flow "Sperry apparatus" (Sperry et al., 1988). Briefly, stem segments at native conductance (K_{native}) were connected via tubing in between a balance and a pressure head of filtered 10 mM KCl. Conductance was calculated as the mass flow of KCl through the sample divided by the pressure gradient. Following measurement of K_{native}, samples were immersed in 10 mM KCl under a vacuum for 24 – 48 hours to remove embolism and were subsequently measured for maximum conductivity (K_{max}). Measurements of K_h were normalized by branch area to derive hydraulic conductivity (K_s), and percent loss of conductivity (PLC) was calculated as $PLC = (1 – (K_s/K_{smax})) \times 100$. Negative PLC values were rare but did occur and were set to zero prior to data analysis.

Quantification of insect and pathogen presence

In November 2018, we felled seven juniper experiencing severe canopy dieback (>50%). These trees were located in areas known to be hotspots of ongoing dieback (Fig. 2). From these trees, we sampled a subset of five bolts (*ca.* 15 cm diameter, 1 m length) that exhibited signs of insect presence (e.g., sap exudation, staining, larval galleries, and frass), which were then brought back to the laboratory and placed in a rearing chamber until insects emerged. As they emerged, insects were morphologically identified using established keys (Furniss and Carolin, 1977; Hammond and Williams, 2013; Westcott, 1990).

One month prior to our stand surveys, we conducted transect surveys for insects and pathogens at two sites experiencing high amounts of canopy dieback (Fig. 2). At each site, a random bearing was chosen and a juniper was sampled in that direction every 20 meters until 16 trees were sampled. For each sampled tree, percent canopy dieback was visually estimated and trees were assessed for symptoms and signs associated with forest insects and diseases common to piñon-juniper woodland communities. Heartwood and sapwood were examined for signs of insect and pathogen presence, including sap exudation, staining, larval galleries, and frass. In cases of wood boring larvae, insects were identified to family and not to species based on the shape of larvae head capsule and gallery. The presence or absence of mistletoe on sampled trees was also noted during these surveys. All insect and pathogen identification was done using morphological keys (Furniss and Carolin, 1977; Hammond and Williams, 2013; Westcott, 1990).

Fig. 2. Map of field sites with coordinates. Red dots represent sites selected for stand surveys and physiological measurements, while yellow dots represent sites where insect and pathogen samples were collected.



Climate and soils data

Monthly climate data for each plot were obtained from the 4 km PRISM data product (prism.oregonstate.edu). Each plot was located in a separate PRISM grid cell. Soil property data for each plot were obtained from the dataset of Nauman and Duniway (2020), including available water capacity, bulk density, soil texture, rock fragment volume (all at depths of 0, 5, 15, 30, 60, 100, and 200 cm), and depth to restrictive layer. Briefly, this approach expands on existing soil mapping efforts by training a random forest algorithm on field observations of soil properties and a wide variety of covariates related to site climate, topography, geology, and vegetation. These relationships are then used to interpolate soil properties in between field observations.

Statistical analyses

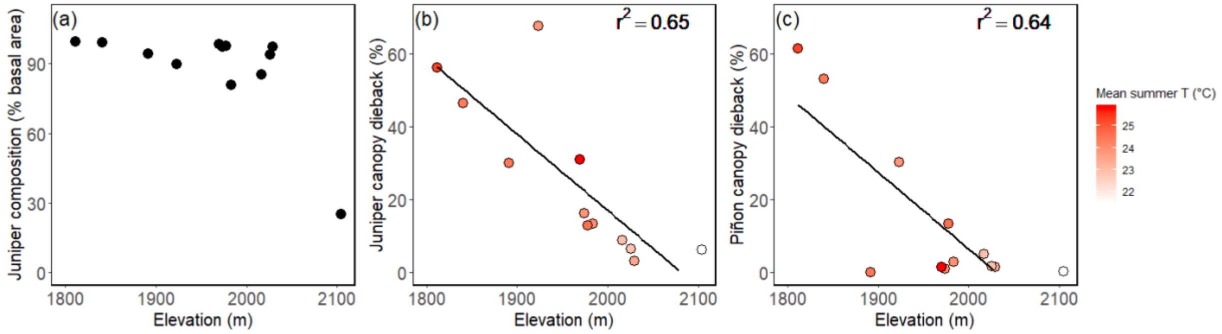
We assessed relationships between tree- and stand-level dieback and various physiological, demographic, topographic, and climatic drivers via ordinary least squares regression. K_s and K_h data were natural log transformed and canopy dieback data were square root transformed (since dead foliage estimates on focal trees were frequently zero) prior to analysis in order to improve the normality and homoscedasticity of residuals. These assumptions were confirmed for all other variables using quantile-quantile plots. We fit generalized linear models of juniper dieback using the R package *lme4* (Bates et al., 2015). The full model included all likely explanatory variables (elevation, plot basal area, predawn and midday water potentials, native K_s, PLC, and interactions between elevation and every other term). We selected the model with the lowest AIC value (Akaike Information Criterion) via stepwise addition and removal of predictors using the function *step()* in the R package *stats* (R Core Team 2019). Due to issues of co-linearity, we elected to only use native K_s and not maximum K_s or native/maximum K_h in our model selection. All analyses were conducted in R 3.6 (R Core Team 2019).

Results

Dieback following the 2018 drought

Canopy dieback was rapid, severe, and highly spatially variable following the 2018 drought. In May of 2019, we observed juniper dieback exceeding 60% in some stands, whereas dieback was nearly non-existent in other areas (Fig. 3b). Severe dieback was extremely common, as 18% of all measured junipers had >80% canopy dieback, though only 6% of trees with some dieback were entirely dead (100% canopy dieback). Some piñon dieback was observed (Fig. 3c), though most of our plots were dominated by juniper (Fig. 3a) and thus this piñon dieback represented a small percentage when scaled to the whole stand. This dieback remained static throughout 2019 – both individual-level dieback (from the focal trees selected for targeted monitoring, $r^2 = 0.91$, $p < 0.0001$) and stand-level means for both species (juniper: $r^2 = 0.97$, $p < 0.0001$, piñon: $r^2 = 0.96$, $p < 0.0001$) were highly correlated between May and October stand surveys, and the slope of this relationship did not deviate from 1. Thus, for all subsequent analysis we use stand survey data collected in May 2019.

Fig. 3. Relationships between site elevation and (a) juniper species composition, (b) juniper canopy dieback, and (c) piñon canopy dieback. Color of points represents the summer (June – August) temperature during the 2018 drought at each site (˚C).



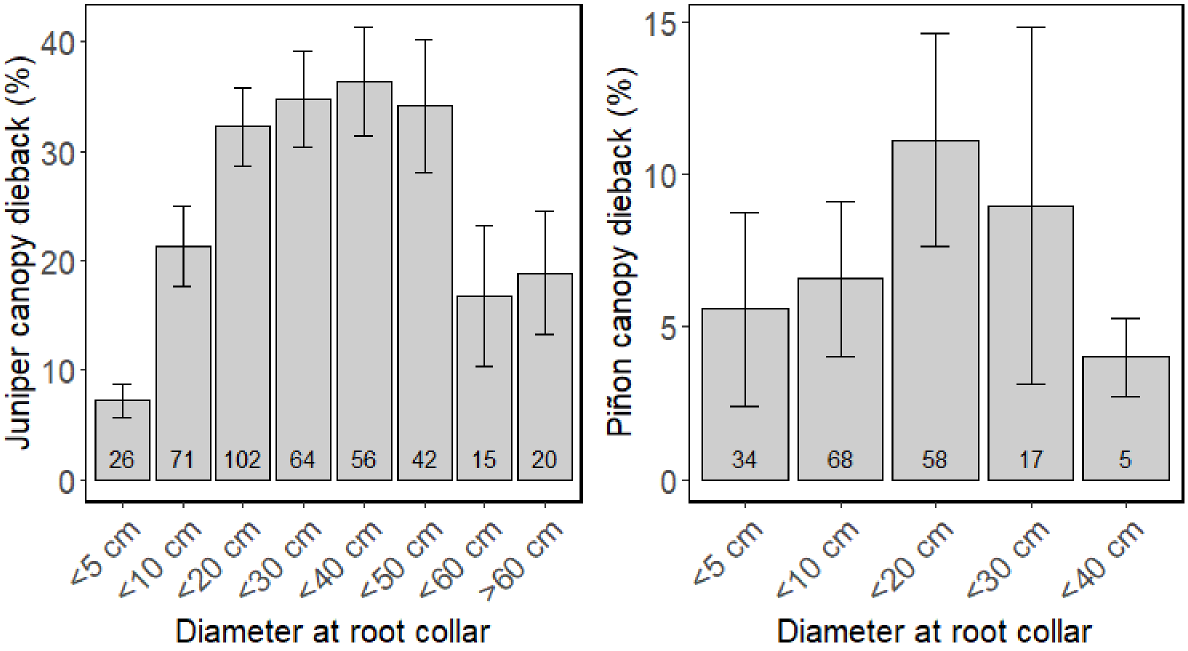
Topographic, edaphic, climatic, and demographic drivers of dieback

Tree dieback was strongly associated with gradients in elevation and temperature across our plots, as both juniper (Fig. 3b, $r^2 = 0.65$, $p = 0.001$) and piñon dieback (Fig. 3c, $r^2 = 0.64$, $p = 0.001$) was most severe at low elevation sites. Stand-level juniper dieback was positively related to mean site temperature (20-year mean to account for recent climate shifts) in winter (January – March, $r^2 = 0.43$, $p = 0.02$), spring (April – May, $r^2 = 0.36$, $p = 0.04$), and summer (June – August, $r^2 = 0.34$, $p = 0.04$). Dieback was not consistently associated with other climatic factors such as vapor pressure deficit or precipitation (neither historical means nor during the 2018 drought). Likewise, dieback of either species was not significantly related to basal area ($p = 0.77$).

Juniper dieback was not associated with any edaphic qualities, as no consistent correlations existed across soil depths between stand-level juniper dieback and available water capacity, bulk density, soil texture, rock fragment volume, or depth to restrictive layer.

Foliage dieback in junipers tended to be highest in trees that were 10 – 60 cm in diameter at root collar (DRC), while the smallest and largest individuals largely escaped severe dieback (Fig. 4a). Piñon dieback did not exhibit similar size class trends (Fig. 4b).

Fig. 4. Observed dieback in various size classes of (a) juniper and (b) piñon. Error bars represent ± standard error and numbers represent the sample size in each size class.

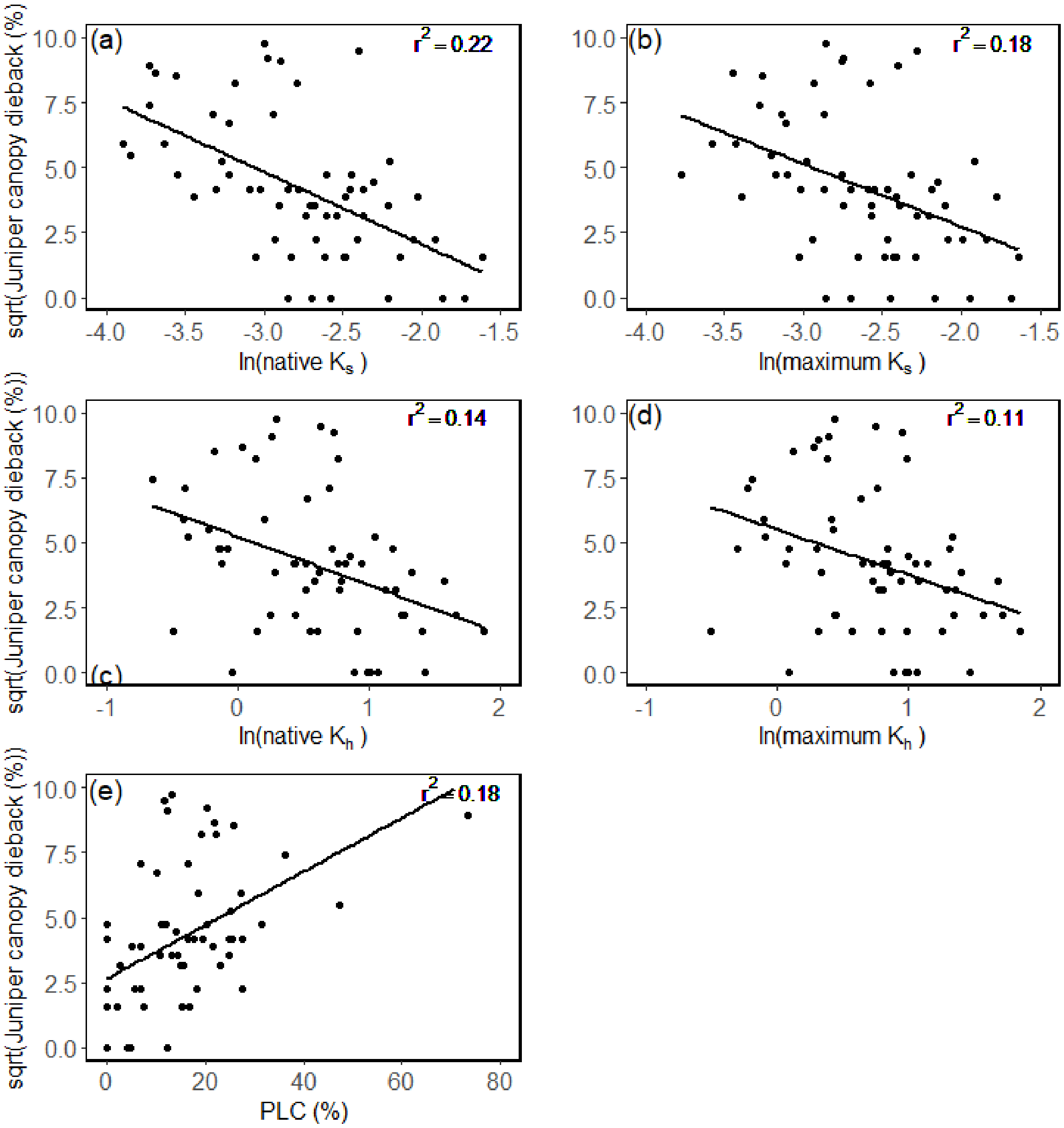


Role of tree hydraulics in juniper dieback

We observed large variability in predawn (-0.7 – -1.7 MPa) and midday (-1.8 – -3.6 MPa) leaf water potentials, indicative of variation in both water access and leaf-level responses to weather variability across the region. However, we found that the linkages between water potential and juniper dieback were weak and differed depending on sampling time. In May, dieback was negatively related to predawn leaf water potential ($r^2 = 0.15$, $p = 0.001$) but not to midday leaf water potential ($p = 0.16$), while in July, dieback was not significantly related to midday ($p = 0.07$) or predawn ($p = 0.64$) leaf water potential.

We did find links between July water potentials, PLC, and dieback, as there was a significant negative relationship between midday leaf water potential and PLC ($r^2 = 0.12$, $p = 0.007$) and a positive relationship between PLC and juniper dieback (Fig. 5e, $r^2 = 0.18$, $p = 0.0008$). Maximum and minimum hydraulic conductivity (K_s) and conductance (K_h) were negatively related to juniper dieback (Fig. 5a-d).

Fig. 5. Relationships between juniper canopy dieback and (a) native conductivity, (b) maximum conductivity, (c) native conductance, (d) maximum conductance, and (e) percent loss of conductivity.



Our model selection analysis indicated that stand-level juniper dieback was best explained by a combination of elevation, predawn water potential, native K_s, PLC, and the interactions between elevation and basal area, native K_s, and PLC (Table S1, Cox and Snell pseudo $r^2 = 0.44$). All of the coefficients in our optimized model qualitatively matched the bivariate relationships previously described (i.e., dieback was positively related to PLC and negatively related to elevation).

Insect and pathogen dynamics

Buprestidae spp. larvae and two adult *Semanotus ligneus* were initially identified in the field in 2018. Following 176 days in a rearing chamber, 11 adult *Chrysobothris texana* had emerged from the subset of five sampled juniper bolts. No evidence of other insects was observed in the year following the emergence of *C. texana*.

In transects selected for insect and pathogen sampling in 2019, we found that only 41% of trees exhibiting significant canopy dieback (>25%) also had symptoms or signs associated with the presence of biotic agents. We found increased presence of round-headed (*Cerambycidae*) and flat-headed (*Buprestidae*) woodboring beetles, bark beetles (*Phloeosinus* spp.), other insects (*Walshomyia juniperina*), and stem rot in junipers that displayed significant canopy dieback, though this trend was only apparent at one site (Table 1). Out of the juniper samples that had biotic agents present, nearly half of those were biotic agents other than woodborers. Juniper foliage dieback was associated with biotic agents in only 8% of all samples. Juniper mistletoe (*Phoradendron juniperum*) was the most commonly observed non-woodborer biotic agent but was largely apparent in healthy trees via our insect and pathogen transect sampling. We found that 5.6% of surveyed junipers had visible signs of *Phoradendron juniperum*, yet these trees actually had significantly lower canopy dieback than unaffected junipers ($p < 0.0001$). Stem rot was only apparent in 20% of trees with substantial (>25%) canopy dieback at one site.

Table 1. Summary of insect and pathogen analysis of juniper trees sampled via transects in 2019. Superscript letters indicate genus and/or species (if known): ^{a}*Buprestidae* or *Cerambycidae* spp., ^{b}*Phloeosinus* spp., ^{c}*Walshomyia juniperina*, ^{d}*Phoradendron juniperinum*, ^{e}unidentified stem rot. Bins of greater than or less than 25% canopy dieback was selected here as it represented the upper quartile of

dieback estimates and corresponded to the threshold below which low conductivity and conductance values were associated with high canopy dieback. We note that some individuals had more than one biotic agent present.

	Juniper dieback			**Woodborers**	**Other insects**	**Mistletoe**	**Stem rot**
Site	*% canopy dieback*	*n* – total	*n* – biotic agents present		*% presence*		
Alkali Ridge	0 – 25	12	2	8.3^{a}	0	16.7^{d}	0
	26 – 100	14	5	28.6^{a}	7.1^{b}	0	0
Cedar Mesa	0 – 25	10	6	30^{a}	40^{c}	30^{d}	0
	26 – 100	15	7	20^{a}	20^{c}	0	20^{e}

Discussion

Mortality of piñon pine following drought in the American southwest has become a common occurrence in recent decades that follows a well-established etiology: piñons tend to die off following drought over the course of a few years due to a combination of hydraulic damage and resulting attack from *Ips confusus*. However, the 2018 drought in southeastern Utah has brought on a novel dieback event: rapid and severe canopy death in typically more drought-tolerant juniper associated with the acute effects of drought.

Juniper canopy dieback was most severe at hot, low elevation sites, where the effects of drought are exacerbated due to enhanced atmospheric water demand and resultant stress at the leaf-level (Grossiord et al., 2020). Elevation gradients in mortality have been previously documented in piñon (Clifford et al., 2011; Martens et al., 2001) and tend to be a global pattern in drought-driven tree mortality episodes, reflecting that climate stress has likely overwhelmed the acclimation and adaptation levels of trees at drier locations (Anderegg et al., 2019). However, the degree to which low elevation piñon died during the 2018 drought remains to be seen. While we did observe an elevation gradient in piñon canopy dieback, this trend was largely driven by the death of the few piñons present in our lowest elevation sites. Thus, a larger sample size is needed to make robust conclusions regarding the fate of low elevation piñon. The possibility exists that the piñons remaining at these low elevation sites are especially well situated to survive drought due to access to deep sources of moisture (i.e., “hydraulic refugia”, Mackay et al., 2020; McDowell et al., 2019; Ripullone et al., 2020).

Juniper dieback was associated with significant amounts of hydraulic damage in branch xylem, further implicating drought stress as the primary causal agent behind this canopy dieback. We do note that we found PLC in trees with significant dieback to be generally lower than is usually observed to cause mortality (Adams et al., 2017). This could be due to a result of our sampling approach whereby we selected foliage that was representative of whole-tree dieback. If the sectorial behavior of junipers causes the loss of whole branches to balance water supply with demand, then sampling living branches may underestimate the hydraulic impairment of the whole tree. We also observed dieback to be highest in trees with low maximum and native conductivity. Other studies have thoroughly linked elevated risk of mortality to low native conductivities and high PLC (Anderegg et al., 2015, 2013). However, we additionally found that canopy dieback was linked to maximum conductivity. Tree hydraulic status is a careful balance between water supply in soil, demand from leaves, and the ability of xylem to link demand with supply. Low maximum conductivity could indicate an inability of existing xylem to supply water to the canopy during drought, perhaps as a result of accumulated drought damage from previous droughts, and thus lead to eventual dieback of foliage.

The historical drought tolerance of juniper has been assumed to be partially due to its high resistance to embolism (Koepke and Kolb, 2013; West et al., 2007b). However, it is uncertain if this embolism resistance confers drought tolerance through increased hydraulic safety (Plaut et al., 2012) or merely allows junipers to adopt an anisohydric so the tree can function longer under severe water deficits yet still accrue hydraulic damage (Kannenberg et al., 2019; McDowell et al., 2008; West et al., 2008). While our results cannot resolve this debate, our data do indicate that juniper trees were pushed to their hydraulic limit, and the observed links between elevation, climate, hydraulic function, and dieback demonstrate that juniper canopy dieback was caused by the effects of the 2018 drought.

Past droughts in this region have been followed by large insect outbreaks in piñon, which ultimately caused mortality (Clifford et al., 2008; Gaylord et al., 2015; Meddens et al., 2015). However, we did not observe increased presence of insects and pathogens to be linked to canopy dieback in juniper. Moreover, none of the insects or pathogens identified are considered major primary agents, as high densities of these agents largely indicate declining host tree conditions (Gaylord et al., 2013; Ray et al., 2019). The species of woodborers that emerged from our rearing chambers (*Chrysobothris texana*), as well as the families of woodborer found in the field (*Buprestidae* and *Cerambycidae*), are commonly found in declining junipers throughout the southwest, yet little information is known regarding their ecology (Westcott, 1990). While some species in these families will attack and kill healthy trees, most are not known to do so and instead will attack stressed, dying, and dead trees (Furniss and Carolin, 1977; Gaylord et al., 2013; Ray et al., 2019; Westcott, 1990). Likewise, our transect sampling in 2019 revealed the presence of woodboring beetles (*Buprestidae* and *Cerambycidae)* and other insects (the bark beetle *Phloeosinus* spp. and the gall midge *Walshomyia juniperina)*, though their presence was not consistently higher in trees with significant canopy dieback across sites. While we did find increased presence of stem rot at one site in junipers with significant canopy dieback, this was likely a secondary consequence of tree dieback instead of a primary cause. The final biotic agent we observed was juniper mistletoe (*Phoradendron juniperinum*). While juniper mistletoe can exacerbate drought stress by causing water loss in heavily infected trees, we found its presence was actually higher in healthy trees. Given the methods used, the observed presence of insects and pathogens is likely a conservative estimate. However, the insects and pathogens we did observe are not known to be primary agents of tree mortality, nor was their presence consistently elevated in trees with canopy dieback, further strengthening our conclusions that this novel dieback event was primarily driven by recent drought stress.

Spatially heterogenous dieback could be due to variation in demographic characteristics such as basal area, tree age, and size. However, these links are far from conclusive, as previous outbreaks of piñon mortality have been found to be both density-dependent (Greenwood and Weisberg, 2008; Negrón and Wilson, 2003) and density-independent (Clifford et al., 2008; Floyd et al., 2009). Our results indicate that neither piñon nor juniper dieback was density-dependent at our sites. Taken in context with previous research, we suggest that both the severity of drought and the incidence of insects or pathogens could be key factors that dictate the density-dependence of mortality. Density-dependence of mortality likely arises due to competition for water (Young et al., 2017) and/or the population dynamics of insects for stands that are dense in hosts (Negrón and Wilson, 2003). In severe droughts like the one in 2018, water stress could be so drastic as to overwhelm the influence of competition, and thus in the absence of insects or pathogens that prefer dense stands, there is no *a priori* reason why density-dependence of drought susceptibility should occur (Floyd et al., 2009). It has been suggested that reducing forest basal area could serve as a key management strategy to reduce climate change-induced tree mortality (Bradford and Bell, 2017; Sohn et al., 2016). While our data speak only to the influence of natural variation in basal area (not to the benefits of artificial manipulations in stand density), our results indicate that the benefits of reductions in basal area are likely to be highly context-dependent and may only become apparent during moderate droughts in species that are susceptible to the density-dependent influence of insects and pathogens.

Insect/pathogen host selection also explains the size-dependent piñon mortality of the past, where the largest trees have been preferred by *Ips confusus* and died at much higher rates (Floyd et al., 2009; Meddens et al., 2015). We did not observe such a size-related trend in piñon dieback, as all size classes experienced canopy dieback at similar rates. Since juniper dieback is historically rare, few studies exist documenting the size-dependence of its dieback. We found that intermediate size classes of juniper (between 20 and 60 cm DRC) had the highest rates of canopy dieback. The survival of small junipers could be explained from a physiological perspective (whereby smaller trees are more resistant to drought) or from a facilitation perspective (whereby small junipers are associated with “nurse plants” that provide a more favorable microclimate). Juniper recruitment is generally not known to be dependent on the presence of larger vegetation to provide the sapling with a more favorable microclimate (Redmond et al., 2018, 2015; Redmond and Barger, 2013), but in some cases small trees can be more drought tolerant than larger individuals (Bennett et al., 2015; Grote et al., 2016; Merlin et al., 2015). The largest junipers we measured were highly sectorial and consisted of multiple stems. Thus, these trees may have been so well established and had such an extensive root system that their drought tolerance was enhanced. More research into the physiology and spatial patterns of the remaining healthy junipers is especially pressing as the drought tolerance of these individuals will dictate stand dynamics in the coming decades, as will the recruitment and growth of new trees. Unfortunately, regeneration of these species is particularly difficult at the hot and dry sites where juniper dieback was the greatest (Redmond et al., 2018).

Multiple years of drought have been previously found to be necessary to cause canopy dieback in juniper (Gaylord et al., 2013), yet we observed large amounts of canopy dieback within months following a severe drought. This dieback had progressed to whole tree mortality in only a small number of cases, though longer-term monitoring is necessary in order to link this dieback to either recovery or mortality. While dieback did not seem to be worsening during 2019, the fate of these trees during future periods of water stress remains to be seen. Juniper trees are highly sectorial and most mature individuals will have branches completely devoid of foliage. While the possibility exists that recent canopy dieback represents an adjustment to leaf area in order to cope with decreased water supply, evidence indicates that leaf area:sapwood area ratios are unlikely to change in surviving drought-stressed juniper (McBranch et al., 2018). Currently, the degree to which canopy dieback foreshadows eventual mortality of the entire tree is unknown (Gaylord et al., 2013; Plaut et al., 2013). Nevertheless, the high proportion of juniper trees exhibiting large amounts of canopy dieback is a dire indicator for declining juniper health in the coming years.

At face value, this dieback seems consistent with the numerous drought-induced mortality events worldwide (Allen et al., 2015, 2010). However, a crucial unanswered question remains: why juniper, and why now? Perhaps an increase in the frequency and severity of stressors, including the 19-year megadrought punctuated by multiple global change type droughts, has pushed these trees to a tipping point. Crucially, this dieback could serve as a positive feedback on decreasing water availability and further hasten the loss of piñon-juniper woodlands (Morillas et al., 2017). Accurately projecting the fate of piñon-juniper woodlands hinges on understanding the causal mechanisms behind this juniper canopy dieback, and how these mechanisms of dieback may be exacerbated by future climatic changes. Is this a one-time dieback event that will be rectified by juniper regeneration, or the start of a widespread disappearance of low elevation piñon-juniper woodlands (Friggens et al., 2012)? The dieback event presented here serves as a ‘leading edge’ for climate change impacts in the region and an important case study for understanding the threats to dryland ecosystems as they continue to warm and dry (Bradford et al., 2020; Hoover et al., 2020).

Acknowledgements

We are especially grateful to Kay Shumway for noticing the dieback in 2018 and notifying a wide range of interested organizations. Insect and pathogen sampling was assisted by Forest Health Protection Ogden/Gunnison field office staff, the Bureau of Land Management Monticello District Office, the Manti-La Sal National Forest Moab/Monticello Ranger Districts, and Dana Witwicki (National Park Service). Rick

Westcott and the Oregon Department of Agriculture were crucial for their buprestid taxonomy expertise. We also would like to thank Kelly Kerr and Kristian Knuths for attending the initial site scouting trip and assisting with preliminary data collection, Jaycee Cappaert, Derek Kober, and Martin Venturas for assisting with hydraulics measurements, and Travis Nauman and Mike Duniway for helping with soils data. WRLA was supported by the David and Lucille Packard Foundation, the US National Science Foundation grants #1714972 and #1802880, and the USDA National Institute of Food and Agriculture, Agricultural and Food Research Initiative Competitive Program, Ecosystem Services and Agro-Ecosystem Management, grant #2018-67019-27850. SAK is supported by the NSF DEB Ecosystem Science cluster grant #1753845. Funding for this project was provided by the USDA Forest Service Forest Health Protection Evaluation Monitoring program grant #19-05.

References

Abatzoglou, J.T., Dobrowski, S.Z., Parks, S.A., Hegewisch, K.C., 2018. TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958-2015. Sci. Data 5, 1–12. https://doi.org/10.1038/sdata.2017.191

Adams, H.D., Zeppel, M.J.B., Anderegg, W.R.L., Hartmann, H., Landhäusser, S.M., Tissue, D.T., Huxman, T.E., Hudson, P.J., Franz, T.E., Allen, C.D., Anderegg, L.D.L., Barron-gafford, G.A., Beerling, D.J., Garcia-forner, N., Gaylord, M.L., Germino, M.J., Gessler, A., Hacke, U.G., Law, D.J., Lewis, J.D., Limousin, J., Love, D.M., Macalady, A.K., Plaut, J.A., Pockman, W.T., Quirk, J., Reinhardt, K., Ripullone, F., 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. Nat. Ecol. Evol. 1, 1285–1291. https://doi.org/10.1038/s41559-017-0248-x

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6, 1–55. https://doi.org/10.1890/ES15-00203.1

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Anderegg, W.R., Anderegg, L.D., Kerr, K.L., Trugmna, A.T., 2019. Widespread drought-induced tree mortality at dry range edges indicates that climate stress exceeds species' compensating mechanisms. Glob. Chang. Biol. 25, 3793–3802.

Anderegg, W.R.L., Flint, A., Huang, C., Flint, L., Berry, J.A., Davis, F.W., Sperry, J.S., Field, C.B., 2015. Tree mortality predicted from drought-induced vascular damage. Nat. Geosci. 1–5. https://doi.org/10.1038/NGEO2400

Anderegg, W.R.L., Plavcová, L., Anderegg, L.D.L., Hacke, U.G., Berry, J.A., Field, C.B., 2013. Drought's legacy: Multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. Glob. Chang. Biol. 19, 1188–1196. https://doi.org/10.1111/gcb.12100

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Bennett, A.C., McDowell, N.G., Allen, C.D., Anderson-Teixeira, K.J., 2015. Larger trees suffer most during drought in forests worldwide. Nat. Plants 1, 15139. https://doi.org/10.1038/nplants.2015.139

Bestelmeyer, B.T., Okin, G.S., Duniway, M.C., Archer, S.R., Sayre, N.F., Williamson, J.C., Herrick, J.E., 2015. Desertification, land use, and the transformation of global drylands. Front. Ecol. Environ. 13, 28–36. https://doi.org/10.1890/140162

Bowker, M.A., Muñoz, A., Martinez, T., Lau, M.K., 2012. Rare drought-induced mortality of juniper is enhanced by edaphic stressors and influenced by stand density. J. Arid Environ. 76, 9–16. https://doi.org/10.1016/j.jaridenv.2011.08.012

Bradford, J.B., Bell, D.M., 2017. A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area. Front. Ecol. Environ. 15, 11–17. https://doi.org/10.1002/fee.1445

Bradford, J.B., Schlaepfer, D.R., Lauenroth, W.K., Palmquist, K.A., 2020. Robust ecological drought projections for drylands in the 21st century. Glob. Chang. Biol. 26, 3906–3919. https://doi.org/10.1111/gcb.15075

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. U. S. A. 102, 15144–15148. https://doi.org/10.1073/pnas.0505734102

Campbell, M.J., Dennison, P.E., Tune, J.W., Kannenberg, S.A., Kerr, K.L., Codding, B.F., Anderegg, W.R.L., 2020. A multi-sensor, multi-scale approach to mapping tree mortality in woodland ecosystems. Remote Sens. Environ. 245, 111853. https://doi.org/10.1016/j.rse.2020.111853

Clifford, M.J., Cobb, N.S., Buenemann, M., 2011. Long-Term Tree Cover Dynamics in a Pinyon-Juniper Woodland: Climate-Change-Type Drought Resets Successional Clock. Ecosystems 14, 949–962. https://doi.org/10.1007/s10021-011-9458-2

Clifford, M.J., Rocca, M.E., Delph, R., Ford, P.L., Cobb, N.S., 2008. Drought induced tree mortality and ensuing bark beetle outbreaks in Southwestern pinyon-juniper woodlands. Ecol. Manag. Restor.

pinon-juniper Ponder. pine Ecosyst. Comb. Proc. 2005 St. Georg. Utah 2006 Albuquerue, New Mex. Work. 39–51.

Cook, B.I., Ault, T.R., Smerdon, J.E., 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Sci. Adv. 1. https://doi.org/10.1126/sciadv.1400082

Dai, A., 2013. Increasing drought under global warming in observations and models. Nat. Clim. Chang. 3, 52–58. https://doi.org/10.1038/nclimate1633

Floyd, M.L., Clifford, M., Cobb, N.S., Hanna, D., Delph, R., Ford, P., Turner, D., 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon - Juniper woodlands. Ecol. Appl. 19, 1223–1230. https://doi.org/10.1890/08-1265.1

Friggens, M.M., Warwell, M. V., Chambers, J.C., Kitchen, S.G., 2012. Modeling and predicting vegetation response of western USA grasslands, shrublands, and deserts to climate change. USDA For. Serv. - Gen. Tech. Rep. RMRS-GTR 1–20.

Furniss, R., Carolin, V., 1977. Western forest insects. U.S.D.A. Forest Service Misc. Publ. 1339.

Gaylord, M.L., Kolb, T.E., McDowell, N.G., 2015. Mechanisms of piñon pine mortality after severe drought: a retrospective study of mature trees. Tree Physiol. 35, 806–816. https://doi.org/10.1093/treephys/tpv038

Gaylord, M.L., Kolb, T.E., Pockman, W.T., Plaut, J.A., Yepez, E.A., Macalady, A.K., Pangle, R.E., Mcdowell, N.G., 2013. Drought predisposes piñon-juniper woodlands to insect attacks and mortality. New Phytol. 198, 567–578. https://doi.org/10.1111/nph.12174

Giorgi, F., Im, E., Coppola, E., Diffenbaugh, N., Gao, X., Mariotti, L., Shi, Y., 2011. Higher Hydroclimatic Intensity with Global Warming. J. Clim. 24, 5309–5324. https://doi.org/10.1175/2011JCLI3979.1

Greenwood, D.L., Weisberg, P.J., 2008. Density-dependent tree mortality in pinyon-juniper woodlands. For. Ecol. Manage. 255, 2129–2137. https://doi.org/10.1016/j.foreco.2007.12.048

Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T.W., Sperry, J.S., McDowell, N.G., 2020. Plant responses to rising vapor pressure deficit. New Phytol. https://doi.org/10.1111/nph.16485

Grote, R., Gessler, A., Hommel, R., Poschenrieder, W., Priesack, E., 2016. Importance of tree height and social position for drought-related stress on tree growth and mortality. Trees 30, 1467–1482.

Hammond, H.E.J., Williams, D.J., 2013. Casey’s conundrum, a review of the genus Semanotus Mulsant (Coleoptera: Cerambycidae: Cerambycinae: Callidiini) in North America. Zootaxa 3670, 101–136. https://doi.org/10.11646.zootaxa.3670.2.1

Hoover, D.L., Bestelmeyer, B., Grimm, N.B., Huxman, T.E., Reed, S.C., Sala, O., Seastedt, T.R., Wilmer, H., Ferrenberg, S., 2020. Traversing the Wasteland: A Framework for Assessing Ecological Threats to Drylands. Bioscience 70, 35–47. https://doi.org/10.1093/biosci/biz126

Kannenberg, S.A., Novick, K.A., Phillips, R.P., 2019. Anisohydric behavior linked to persistent hydraulic damage and delayed drought recovery across seven North American tree species. New Phytol. 222, 1862–1872. https://doi.org/10.1111/nph.15699

Koepke, D.F., Kolb, T.E., 2013. Cavitation at a Forest-Woodland Ecotone. For. Sci. 59, 524–535.

Linton, M.J., Sperry, J.S., Williams, D.G., 1998. Limits to water transport in Juniperus osteosperma and Pinus edulis: Implications for drought tolerance and regulation of transpiration. Funct. Ecol. 12, 906–911. https://doi.org/10.1046/j.1365-2435.1998.00275.x

Mackay, D.S., Savoy, P.R., Grossiord, C., Tai, X., Pleban, J.R., Wang, D.R., McDowell, N.G., Adams, H.D., Sperry, J.S., 2020. Conifers depend on established roots during drought: results from a coupled model of carbon allocation and hydraulics. New Phytol. 225, 679–692. https://doi.org/10.1111/nph.16043

Martens, S.N., Breshears, D.D., Barnes, F.J., 2001. Development of species dominance along an elevational gradient: Population dynamics of Pinus edulis and Juniperus monosperma. Int. J. Plant Sci. 162, 777–783. https://doi.org/10.1086/320772

McBranch, N.A., Grossiord, C., Adams, H., Borrego, I., Collins, A.D., Dickman, T., Ryan, M., Sevanto, S., McDowell, N.G., 2018. Lack of acclimation of leaf area:sapwood area ratios in piñon pine and juniper in response to precipitation reduction and warming. Tree Physiol. 39, 135–142. https://doi.org/10.1093/treephys/tpy066

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E. a, 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol. 178, 719–39. https://doi.org/10.1111/j.1469-8137.2008.02436.x

McDowell, N.G., Grossiord, C., Adams, H.D., Pinzón-Navarro, S., Mackay, D.S., Breshears, D.D., Allen, C.D., Borrego, I., Dickman, L.T., Collins, A., Gaylord, M., McBranch, N., Pockman, W.T., Vilagrosa, A., Aukema, B., Goodsman, D., Xu, C., 2019. Mechanisms of a coniferous woodland persistence under drought and heat. Environ. Res. Lett. 14. https://doi.org/10.1088/1748-9326/ab0921

Meddens, A.J.H., Hicke, J.A., Macalady, A.K., Buotte, P.C., Cowles, T.R., Allen, C.D., 2015. Patterns and causes of observed piñon pine mortality in the southwestern United States. New Phytol. 206, 91–97. https://doi.org/10.1111/nph.13193

Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. For. Ecol. Manage. 339, 22–33. https://doi.org/10.1016/j.foreco.2014.11.032

Morillas, L., Pangle, R.E., Maurer, G.E., Pockman, W.T., McDowell, N., Huang, C.W., Krofcheck, D.J., Fox, A.M., Sinsabaugh, R.L., Rahn, T.A., Litvak, M.E., 2017. Tree Mortality Decreases Water Availability and Ecosystem Resilience to Drought in Piñon-Juniper Woodlands in the Southwestern U.S. J. Geophys. Res. Biogeosciences 122, 3343–3361. https://doi.org/10.1002/2017JG004095

Nauman, T.W., Duniway, M.C., 2020. A hybrid approach for predictive soil property mapping using conventional soil survey data. Soil Sci. Soc. Am. J. 1–48. https://doi.org/10.1002/saj2.20080

Negrón, J.F., Wilson, J.L., 2003. Attributes associated with probability of infestation by the pinon ips, Ips confusus (Coleoptera: Scolytidae), in piñon pine, Pinus edulis. West. North Am. Nat. 63, 440–451.

Ogle, K., Whitham, T.G., Cobb, N.S., 2000. Tree-ring variation in pinyon predicts likelihood of death following severe drought. Ecology 81, 3237–3243. https://doi.org/10.1890/0012-9658(2000)081[3237:TRVIPP]2.0.CO;2

Plaut, J.A., Wadsworth, W.D., Pangle, R., Yepez, E.A., McDowell, N.G., Pockman, W.T., 2013. Reduced transpiration response to precipitation pulses precedes mortality. New Phytol. 200, 375–387.

Plaut, J.A., Yepez, E.A., Hill, J., Pangle, R., Sperry, J.S., Pockman, W.T., McDowell, N.G., 2012. Hydraulic limits preceding mortality in a pinon-juniper woodland under experimental drought. Plant, Cell Environ. 35, 1601–1617. https://doi.org/10.1111/j.1365-3040.2012.02512.x

Ray, C., Cluck, D., Wilkerson, R., Siegel, R., White, A., Tarbill, G., Sawyer, S., Howell, C., 2019. Patterns of woodboring beetle activity following fires and bark beetle outbreaks in montane forests of California, USA. Fire Ecol. 15, 21.

Redmond, M.D., Barger, N.N., 2013. Tree regeneration following drought- and insect-induced mortality in piñon-juniper woodlands. New Phytol. 200, 402–412. https://doi.org/10.1111/nph.12366

Redmond, M.D., Cobb, N.S., Clifford, M.J., Barger, N.N., 2015. Woodland recovery following drought-induced tree mortality across an environmental stress gradient. Glob. Chang. Biol. 21, 3685–3695. https://doi.org/10.1111/gcb.12976

Redmond, M.D., Weisberg, P.J., Cobb, N.S., Clifford, M.J., 2018. Woodland resilience to regional drought: Dominant controls on tree regeneration following overstorey mortality. J. Ecol. 106, 625–639. https://doi.org/10.1111/1365-2745.12880

Ripullone, F., Camarero, J.J., Colangelo, M., Voltas, J., 2020. Variation in the access to deep soil water pools explains tree-to-tree differences in drought-triggered dieback of Mediterranean oaks. Tree Physiol. 40, 591–604. https://doi.org/10.1093/treephys/tpaa026

Schenk, H.J., Espino, S., Goedhart, C.M., Nordenstahl, M., Martinez Cabrera, H.I., Jones, C.S., 2008. Hydraulic integration and shrub growth form linked across continental aridity gradients. Proc. Natl. Acad. Sci. U. S. A. 105, 11248–11253. https://doi.org/10.1073/pnas.0804294105

Schwinning, S., Litvak, M.E., Pockman, W.T., Pangle, R.E., Fox, A.M., Huang, C., Mcintire, C.D., 2020. A 3-dimensional model of Pinus edulis and Juniperus monosperma root distributions in New Mexico : implications for soil water dynamics. Plant Soil.

Shaw, J.D., DeBlander, L.T., Steed, B.E., 2005. Forest Inventory and Analysis (FIA) annual inventory answers the question: What is happening to pinyon-juniper woodlands? J. For. 103, 280–285. https://doi.org/10.1093/jof/103.6.280

Sohn, J.A., Saha, S., Bauhus, J., 2016. Potential of forest thinning to mitigate drought stress: A meta-analysis. For. Ecol. Manage. 380, 261–273. https://doi.org/10.1016/j.foreco.2016.07.046

Sperry, J.S., Donnelly, J.R., Tyree, M.T., 1988. A method for measuring hydraulic conductivity and embolism in xylem. Plant. Cell Environ. 11, 35–40.

West, A., Hultine, K., Speryy, J., Bush, S., Ehleringer, J., 2008. Transpiration and hydraulic strategies in a pinyon-juniper woodland. Ecol. Appl. 18, 911–927.

West, A.G., Hultine, K.R., Burtch, K.G., Ehleringer, J.R., 2007a. Seasonal variations in moisture use in a piñon-juniper woodland. Oecologia 153, 787–798. https://doi.org/10.1007/s00442-007-0777-0

West, A.G., Hultine, K.R., Jackson, T.L., Ehleringer, J.R., 2007b. Differential summer water use by Pinus edulis and Juniperus osteosperma reflects contrasting hydraulic characteristics. Tree Physiol. 27, 1711–1720. https://doi.org/10.1093/treephys/27.12.1711

Westcott, R., 1990. Notes on taxonomy, ecology and distribution for some species of Chrysobothris Eschscholtz (Coleoptera: Buprestidae) occurring in the United States (including Hawaii) and Canada. Coleopt. Bull. 44, 323–343.

Williams, A.P., Cook, E.R., Smerdon, J.E., Cook, B.I., Abatzoglou, J.T., Bolles, K., Baek, S.H., Badger, A.M., Livneh, B., 2020. Large contribution from anthropogenic warming to an emerging North American megadrought. Science (80-.). 368, 314–318. https://doi.org/10.1126/science.aaz9600

Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. Ecol. Lett. 20, 78–86. https://doi.org/10.1111/ele.12711