

Canopy foliation and area as predictors of mortality risk from episodic drought for individual trees of Ashe juniper

H. Wayne Polley · Daniel M. Johnson ·
Robert B. Jackson

Received: 3 June 2016 / Accepted: 16 July 2016 / Published online: 26 July 2016
© Springer Science+Business Media Dordrecht (outside the USA) 2016

Abstract Drought is killing an increasing number of trees globally, yet mortality risk remains difficult to predict at fine spatial scales. We sought to identify metrics of living individuals that could be used to estimate mortality risk of Ashe juniper (*Juniperus ashei*) trees and eventually to estimate the fraction of juniper populations at risk from drought. Ashe juniper is a keystone species in the Edwards Plateau region in central Texas, USA. We analyzed tree rings from both living and dead trees to determine growth rate prior to an historic drought in 2011 and measured morphological, physiological, and stand-level variables hypothesized to link growth rate and mortality risk. Slowly growing trees were disproportionately vulnerable to

mortality. Fractional mortality of sampled trees was correlated to the difference between the mean pre-drought basal area increment (BAI) per tree and the predrought BAI of minimally stressed trees growing on deep soil ($=\text{BAI}_{90} - \text{BAI}$). Slowly growing trees had sparsely foliated canopies. $\text{BAI}_{90} - \text{BAI}$ was positively correlated to the difference between: (1) leaf area per unit of projected canopy area per tree (LA) and the LA of minimally stressed trees and (2) projected canopy area (CA) and the CA of comparably sized trees. By contrast, there was no correlation between growth of living trees and light interception by neighboring trees, soil depth, or two functional metrics, the stem–leaf Ψ gradient and leaf light use efficiency. Mortality risk in Ashe juniper populations can be estimated from nondestructive measurements of leaf and canopy area of individual trees using relationships among risk, growth, and leaf and canopy area.

Communicated by William E. Rogers.

Electronic supplementary material The online version of this article (doi:10.1007/s11258-016-0636-3) contains supplementary material, which is available to authorized users.

H. W. Polley (✉)
Grassland, Soil & Water Research Laboratory, USDA–
Agricultural Research Service, Temple, TX 76502, USA
e-mail: wayne.polley@ars.usda.gov

D. M. Johnson
Department of Forest, Rangeland and Fire Sciences,
University of Idaho, Moscow, ID 83844, USA

R. B. Jackson
School of Earth Sciences, Stanford University, Stanford,
CA 94305, USA

Keywords Basal area increment · Canopy area ·
Climate change · Leaf area · Growth rate · Woodland

Abbreviations

| | |
|-------------------|---|
| BA | Basal area (cm ²) |
| BAI | Basal area increment (cm ²) |
| BAI ₉₀ | BAI estimated from a quantile regression (0.90 quantile) model fit to the BAI–canopy area relationship (cm ²) |
| CA | Projected canopy area per tree (m ²) |

| | |
|------------------|---|
| LA | Leaf area per tree (m ²) |
| LA ₉₀ | LA estimated from a quantile regression (0.90 quantile) model fit to the LA–CA relationship (m ²) |
| LAI | Leaf area index |
| PAR | Photosynthetically active radiation |
| PRI | Photochemical reflectance index |

Introduction

Drought-caused tree mortality has impacted large areas in the southern and southwestern USA during recent decades (Allen and Breshears 1998; Schwantes et al. 2016) and is believed to be accelerating globally (Carnicer et al. 2011; Peng et al. 2011; van Mantgem et al. 2009). Mortality-causing droughts may become more common because climate change is anticipated to reduce precipitation and increase the frequency or intensity of drought in several regions globally (IPCC 2013), including the Southern Plains of the USA (US Global Change Research Program 2009). Ecological consequences of extensive woody mortality are numerous and could include reductions in carbon sequestration (Huang et al. 2010), shifts in vegetation ranges (Allen and Breshears 1998), and changes in hydrology (Adams et al. 2012; Zou et al. 2014).

The prospect that climate change will increase the frequency or intensity of mortality-causing droughts has motivated efforts to improve capacity to predict drought vulnerability of trees. These efforts have focused on two general approaches: (1) develop relationships between observed mortality rates and general biotic or abiotic variables, such as stand density, soil depth, and past meteorological conditions (Bowker et al. 2012; Gu et al. 2015; Twidwell et al. 2014) and (2) improve understanding of physiological contributors to tree mortality as a basis for modeling drought vulnerability (Jiang et al. 2013; Williams et al. 2013). Neither of these approaches is strongly predictive of drought vulnerability at fine spatial scales or for individual trees. In order to increase predictive capability, particularly at local scales, for keystone species, and in situations in which mortality is spatially variable, we require readily measureable metrics of living trees that are correlated with vulnerability to drought.

Mortality of individual trees has proven difficult to predict because death represents an end-point response

to cumulative effects of physiological processes, biotic interactions, and climatic and other abiotic drivers and because morphological and physiological indicators of tree vulnerability often are not readily measureable. Several studies, however, have shown that drought disproportionately kills those individuals of a tree species that have been growing most slowly (Ogle et al. 2000; Suarez et al. 2005; Swaty et al. 2004). This relationship between growth rate and mortality risk implicates prior nonextreme stressors of growth, broadly characterized as predisposing stresses (Pedersen 1998), in enhancing vulnerability. For example, prior drought events can predispose trees to mortality risk by reducing tree capacity to transpire and assimilate carbon. The manifestation of predisposing stresses varies among species (Camarero et al. 2015), but often includes shifts in both physiology and morphology. Physiological indicators of vulnerability may include a persistent decline in leaf gas exchange and water potentials and increase in resistance to water transport (Breshears et al. 2009; Pangle et al. 2015). Morphological indicators of vulnerability may include partial defoliation, canopy or branch dieback or, more generally, reduced leaf area (Camarero et al. 2015; Carnicer et al. 2011).

We assessed relationships between (1) mortality of Ashe juniper (*Juniperus ashei* J. Buchholz) trees following an historic drought in the Southern Plains in 2011 and growth rate prior to the drought, and (2) tree growth and both stand-level variables and morphological and physiological attributes of individual trees. Ashe juniper is a keystone woody species in the Edwards Plateau region in west-central Texas, having increased in density since European settlement as a result of overgrazing and fire suppression (Riskind and Diamond 1988; Smeins and Merrill 1988). Density and foliar cover of juniper regulate several ecosystem processes important to management. These include hydrology, forage production for livestock, and wildlife populations, including breeding populations of the endemic and endangered golden-cheeked warbler (*Setophaga chrysoparia*) (Reidy et al. 2016; Taucer et al. 2008). Our primary objective was to identify readily measureable metrics of living juniper individuals that could be used as a surrogate for growth rate to estimate mortality risk under episodic drought. An ultimate aim in doing so is to predict fractional mortality risk of juniper populations at local to larger spatial scales where, as is common, patterns of tree

mortality vary spatially (Twidwell et al. 2014). We hypothesized that: (1) mortality following the 2011 drought was disproportionately expressed among juniper trees that grew slowly during the decade prior to drought, and (2) growth rate among living trees is positively correlated with specific morphological (leaf area, canopy area, and basal area), physiological [leaf water (xylem) potential and photosynthetic light use efficiency], and stand-level variables (soil depth and proximity to neighboring trees).

Materials and methods

Study sites

We studied Ashe juniper trees at two locations in central Texas, USA: Colorado Bend State Park (31°06'N, 98°50'W), located near the city of Lampasas, and an old-field site located near the city of Temple (31°05'N, 97°20'W). Colorado Bend Park is located in the Edwards Plateau region of Texas and is characterized by shallow, stony, clay loam soils underlain by fractured limestone with 1–5 % slopes. The hilly terrain is dominated by Ashe juniper intermixed with oaks and grasses. The old-field site near Temple is characterized by deep clay soil and located near the eastern, high-rainfall extreme of Ashe juniper's distribution. Annual precipitation averages 755 mm (50-year record) and 875 mm (91-year record) at Colorado Bend and Temple, respectively. During the historic drought in 2011, annual precipitation (November through October) was 51 and 41 % of the mean for Colorado Bend and Temple, respectively.

We sampled juniper trees located along 2 sets of perpendicular transects at Colorado Bend Park. Each transect is c. 0.8 km in length. We sampled 45 living and 26 dead trees at Colorado Bend and 15 living trees from along perpendicular transects through the small (approximately 3 ha) old-field site at Temple. Because the old-field is located near the high-precipitation extreme of the species distribution, we assumed that juniper experiences minimal water stress and exhibits near maximal field growth at this site. Tree size may influence vulnerability to drought (Bennett et al. 2015; Suarez et al. 2005; Twidwell et al. 2014); consequently, we selected individuals at both locations that spanned the range of mature tree sizes encountered and were not greatly shaded by neighboring trees.

Growth and morphological variables

Growth per year during the decade prior to (living + dead trees) and period following the 2011 drought (living trees) was determined for each tree by calculating the annual basal area increment (BAI). During 2013–2014, we collected two cores from near the base of the trunk of each tree following measurement of trunk basal diameter. Ashe juniper trees branch near the base requiring that diameter and growth rings be measured at the trunk base. Width of annual growth rings in cores was measured using MeasureJ2X software (VorTech Consulting; Holderness, NH) and a Velmex UniSlide positioning table with AMO Inductive Scale Linear Encoder (Velmex, Inc.; Bloomfield, NY). Ring widths of most individuals varied substantially between low- and high-precipitation years facilitating dating.

Projected canopy area (CA) of each living tree, defined as the surface area projected by the canopy, was calculated from measurements of maximum canopy diameter by assuming that the canopy was circular in shape. Leaf area per tree (LA) was calculated as the product of leaf area index (LAI) and CA, the former derived by measuring tree interception of photosynthetically active radiation using a SunScan canopy analysis system (Delta-T Devices Ltd., Burwell, Cambridge, UK). A remotely sensed estimate of LAI was derived from measurements of the spectral signature of reflected radiation from each tree using an ASD HandHeld2 Pro spectroradiometer (spectral range of 350–1250 nm; ASD Inc., Boulder, CO, USA). We measured reflectance from directly above each tree by suspending the spectroradiometer from a retractable pole at a height sufficient to include 50–75 % of CA of the tree in the field of view of the instrument. Reflectance was measured on cloudless days within 2 h of solar noon. Measurements were referenced to a standard barium sulfate panel at c. 15-min intervals to maintain consistency in observations.

We found that maximum values of the 10-year, predrought average of BAI per tree increased as a linear function of the CA of sampled trees. We considered near 'maximum' values of BAI as equal to values at the 90th percentile of a quantile regression fit to the BAI-CA relationship (BAI₉₀). Quantile regression is a technique used to determine relationships between variables for different portions of a

probability distribution (Cade and Noon 2003). Tree growth follows a sigmoidal curve, such that growth per unit of tree size (growth rate) is age- or size-dependent (Weiner and Thomas 2001). We standardized measurements of juniper growth and LA for tree size by comparing ‘maximum’ and observed values of BAI and LA at a common CA. Accordingly, a size-standardized estimate of growth deviation from near maximum was calculated for each living and dead tree by subtracting observed BAI from the BAI_{90} estimated from quantile regression for a tree with the same CA ($BAI_{90} - BAI$). A similar approach was taken to calculate a size-standardized estimate of LA deviation from maximum LA ($LA_{90} - LA$). LA deviation was calculated for each living tree by subtracting the observed LA from the LA estimated for a tree with the same CA from a 0.9 regression quantile model fit to the relationship between LA and CA for all living trees combined.

Physiological and stand-level variables

During summers in 2014–2015, we measured the gradient in water potential between the leaf (Ψ_{leaf}) and stem of juniper (Ψ_{stem}) as an index of resistance to water flow in the stem (Begg and Turner 1970). Liquid phase transport through the stem is proportional to the Ψ gradient across the stem and inversely proportional to stem resistance to water flow. For a given rate of water transport and, by inference of transpiration, stem resistance to transport must increase if the stem–leaf gradient in Ψ increases. We expected the Ψ gradient to increase as Ψ_{leaf} declined and to be greater among sparsely than more fully foliated trees.

Juniper leaves are small, scale-like and arranged in whorls. We used a pressure chamber to measure xylem (water) potential of two sun-exposed leaf whorls (hereafter, leaves) from the outer edge of the canopy of each of 45 living trees at Colorado Bend (Ψ_{leaf}). Concurrently, we estimated Ψ_{stem} by measuring Ψ of two leaves per tree from a branch that had been enclosed late the prior afternoon in a reflective insulation sleeve (Reflectix[®], Markleville, IN, USA) to eliminate transpiration (Begg and Turner 1970). We measured incident photosynthetically active radiation (PAR) on a plane horizontal to the soil surface at each tree.

Drought could reduce stomatal conductance and leaf photosynthesis by reducing Ψ_{leaf} (Pangle et al.

2015). Prior to each measurement of Ψ , we measured the photochemical reflectance index (PRI) on bagged and sunlit leaves of juniper as an index of photosynthetic light use efficiency (Gamon et al. 1997), where

$$PRI = \frac{R_{531} - R_{570}}{R_{531} + R_{570}}, \quad (1)$$

and R_{531} and R_{570} indicate reflectance at 531 and 570 nm, respectively. Reflectance at 531 nm declines as leaves dissipate absorbed energy in excess of that required for photosynthesis. PRI is positively correlated with net photosynthesis (Gamon et al. 1997), and by inference, with stomatal conductance. PRI was derived by measuring the spectral signature of reflected radiation from leaves on which water potential was subsequently measured. Reflectance was measured using an ASD Fieldspec 3 spectroradiometer with a spectral range of 350–2500 nm and spectral resolution of 3 nm at 700 nm (ASD Inc., Boulder, CO, USA). Reflectance was measured on intact leaves using the light source associated with the ASD Inc. ‘leaf clip.’

Maximum soil depth at each tree was taken as the average depth to which a metal rod could be hammered into soil at cardinal positions around the tree dripline. We measured average interception of incident PAR at 1 m distance from the canopy edge of each target tree. Values of PAR interception at cardinal positions around each tree were averaged as an index of stand density.

Statistics

Quantile regression was used to estimate near maximal rates of change in two dependent variables, BAI and LA, as a function of CA (Cade and Noon 2003). We consider near ‘maximum’ values of BAI and LA as equal to values at the 90th percentile of the distribution of these dependent variables conditional on values of CA. Partial least-squares regression (PLSR) analysis was used to develop a predictive model for tree LAI from measurements of spectral reflectance. PLSR permits use of the continuous spectrum of reflectance measurements in prediction and accommodates strong collinearity among spectral signals by reducing the number of predictor signals to a smaller set of uncorrelated components (Wold et al. 1984). Bivariate and multiple regression analyses were used to assess relationships between dependent

variables, such as the absolute or relative deviation of growth (BAI) from maximum values (BAI_{90}), and various morphological, physiological, and stand-level predictor variables. Analyses were conducted with SAS 9.3 (Littell et al. 2002).

Results

Links among growth, leaf and canopy area, and drought mortality

Maximum values of annual BAI averaged over the decade prior to the 2011 drought were linearly correlated to CA of juniper (Fig. 1). 90 % of BAI averages were less than or equal to values specified by the BAI versus CA regression line illustrated in Fig. 1 ($=BAI_{90}$). BAI varied by at least an order of magnitude among the 85 trees sampled (living + dead). CA varied by more than a factor of 23 among trees. BAI at a given CA generally was greatest among the trees at Temple that grew on deep soil and received greater annual precipitation during the decade prior to drought than trees at Colorado Bend (mean = 902 and 785 mm at Temple and Colorado Bend, respectively). Predrought means of annual precipitation were similar

to long-term averages at each site (875 and 755 mm, respectively).

Size-standardized values of BAI deviation from maximum ($BAI_{90} - BAI$) ranged from -5.0 to $28.2 \text{ cm}^2/\text{year}$ and clearly were greater on average for dead than living trees (mean \pm SE = 20.1 ± 1.2 and $6.7 \pm 0.7 \text{ cm}^2/\text{year}$, respectively; Fig. 2). These data show that trees growing disproportionately slowly before the drought were more likely to die during or after the drought. Drought killed 87 % (26 of 30) of trees with $BAI_{90} - BAI > 16 \text{ cm}^2/\text{year}$, but 0 % of trees with $BAI_{90} - BAI < 16 \text{ cm}^2/\text{year}$. Mortality was spatially variable and limited to trees with $CA > 20 \text{ m}^2$ among sampled individuals (Fig. 1).

Maximum values of the LA of living trees were linearly correlated to CA (Fig. 3). The difference in LA from a 0.9 regression quantile model fit to the postdrought LA versus CA relationship for all living trees combined ($LA_{90} - LA$) ranged from -59 m^2 (LA exceeded the 0.9 quantile estimate for the observed CA) to 135 m^2 (the LA was 135 m^2 smaller than that of a comparably sized tree at the 0.9 quantile). CA, in turn, was a strong linear function of BA (Table 1). The $BAI_{90} - BAI$ of living trees was a positive, linear function of two predictor variables: $LA_{90} - LA$ (adj. $r^2 = 0.43$, $P < 0.0001$ when 2 outliers were deleted; Fig. 4) and residuals from a CA versus BA regression. A multiple regression

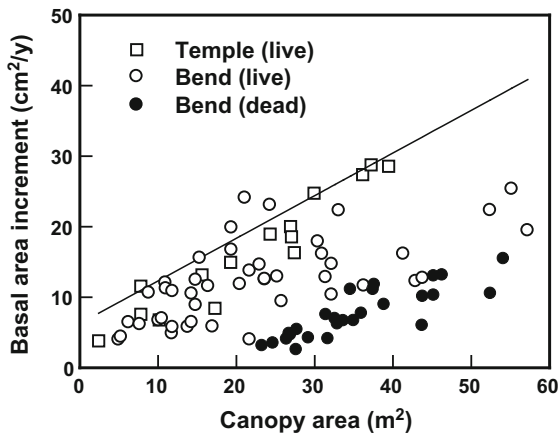


Fig. 1 The average of the annual basal area increment (BAI) for the decade prior to the 2011 drought plotted as a function of the projected canopy area (CA) of Ashe juniper trees that survived (live) and died (dead) following the drought. The CA of dead trees was estimated from a linear regression fit to the CA versus basal diameter relationship of living trees (adj. $r^2 = 0.77$). The solid line is a 0.9 quantile regression fit to the BAI-CA relationship for living trees at Temple and Colorado Bend Park, TX ($P < 0.0001$, $n = 60$)

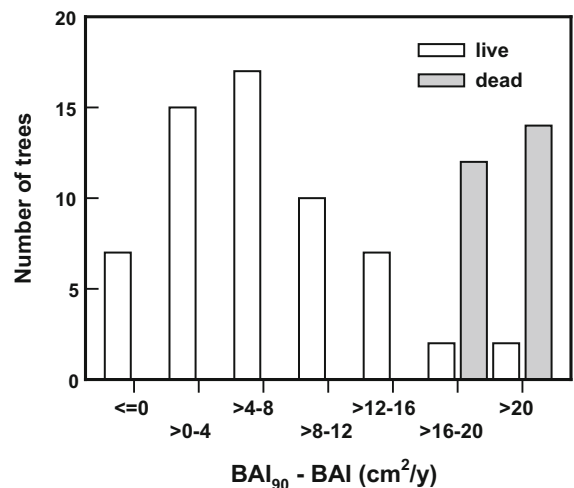


Fig. 2 The number of juniper trees that survived (live) and died (dead) following drought ranked by deviation of the predrought average of BAI from the mean BAI of a similarly sized tree that exhibited near maximal growth ($BAI_{90} - BAI$)

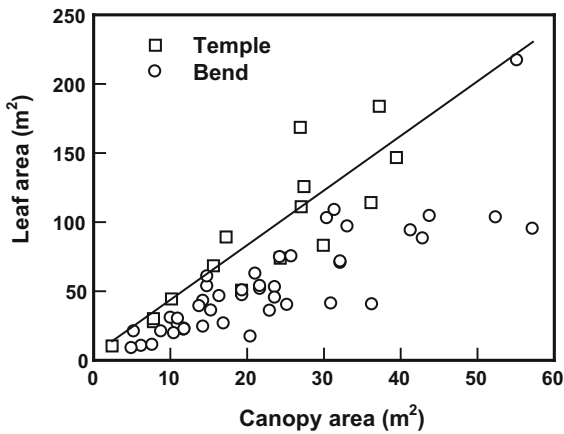


Fig. 3 Leaf area (LA) plotted as a function of the projected canopy area (CA) of currently living juniper trees at Temple and Colorado Bend Park, TX. The solid line is a 0.9 quantile regression fit to the LA–CA relationship ($P = 0.0003$, $n = 60$)

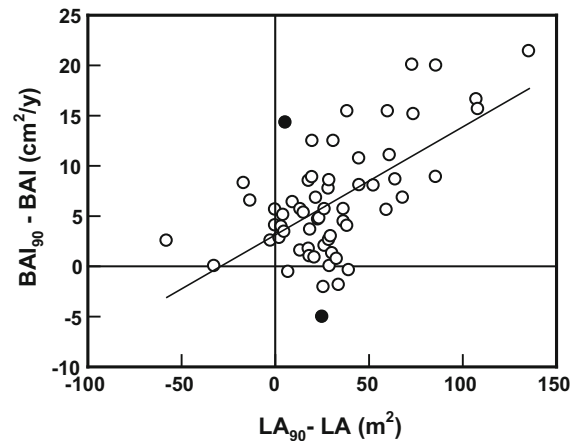


Fig. 4 Size-standardized estimates of the deviation of pre-drought tree growth and of postdrought leaf area from maximum ($BAI_{90} - BAI$ and $LA_{90} - LA$, respectively) were positively correlated for living juniper trees at Temple and Colorado Bend Park. The solid line is a linear regression fit to the growth-leaf area relationship following deletion of the two outliers denoted by closed symbols (adj. $r^2 = 0.43$, $P < 0.0001$, $n = 58$)

equation with both $LA_{90} - LA$ and CA versus BA residuals explained 49 and 55 % of the variance in $BAI_{90} - BAI$ for $n = 60$ and 58 trees (outliers deleted), respectively (Table 1).

Not surprisingly, the link between growth and leaf display was stronger when calculated with contemporary measurements of BAI and LA than with

predrought BAI and postdrought LA. $LA_{90} - LA$ alone explained ≥ 57 % of the variation in $BAI_{90} - BAI$ for 2012, the year following the drought, whether

Table 1 Significant linear relationships of predictor variables with the following dependent variables of Ashe juniper trees—canopy area (CA), the absolute or relative deviation of growth

(BAI) or leaf area per tree (LA) from maximum values (BAI_{90} , LA_{90}), stem-to-leaf Ψ gradient, and the leaf photochemical reflectance index (PRI)

| Dependent variable | Predictor variable(s) | Intercept | Slope(s) | Adj. r^2 | P value | n |
|--|---|-----------|----------|------------|-----------|-----|
| CA (m ²) | BA (cm ²) | 6.934 | 0.017 | 0.77 | <0.0001 | 60 |
| $BAI_{90} - BAI$ (cm ² /year) | $LA_{90} - LA$ (m ²) | 4.117 | 0.076 | 0.49 | <0.0001 | 60 |
| | CA versus BA residuals (m ²) | | 0.388 | | | |
| $BAI_{90} - BAI$ (cm ² /year) | $LA_{90} - LA$ (m ²) | 3.929 | 0.081 | 0.55 | <0.0001 | 58 |
| | CA versus BA residuals (m ²) | | 0.369 | | | |
| $BAI_{90} - BAI$ (2012; cm ² /year) | $LA_{90} - LA$ (2013; m ²) | 5.77 | 0.29 | 0.57 | <0.0001 | 59 |
| $BAI_{90} - BAI$ (2012; cm ² /year) | $LA_{90} - LA_{rs}$ (2013; m ²) | 0.70 | 0.44 | 0.58 | <0.0001 | 59 |
| $(BAI_{90} - BAI)/BAI_{90}$ | $LA_{90} - LA$ (m ²) | 0.253 | 0.002 | 0.09 | 0.01 | 60 |
| $(BAI_{90} - BAI)/BAI_{90}$ | $(LA_{90} - LA)/LA_{90}$ | 0.228 | 0.275 | 0.08 | 0.02 | 60 |
| $(LA_{90} - LA)/LA_{90}$ | fPAR _i by neighbors | 0.59 | -0.40 | 0.22 | 0.0007 | 45 |
| $\Psi_{stem} - \Psi_{leaf}$ (2014; MPa) | Ψ_{stem} (2014; MPa) | 1.11 | 0.18 | 0.19 | 0.002 | 42 |
| $\Psi_{stem} - \Psi_{leaf}$ (2015; MPa) | Ψ_{stem} (2015; MPa) | 0.70 | 0.04 | 0.08 | 0.04 | 43 |
| PRI (2014) | Ψ_{stem} (2014; MPa) | 0.034 | 0.009 | 0.18 | 0.004 | 42 |
| PRI (2015) | Ψ_{stem} (2015; MPa) | 0.016 | 0.004 | 0.15 | 0.006 | 44 |

Date is indicated in parentheses for measurements confined to a single year. fPAR_i by neighbors = the fraction of incident PAR intercepted by neighboring trees. LA was calculated from measurements of PAR interception or remotely sensed readings of spectral reflectance, the latter denoted as LA_{rs}

BA basal area

leaf area per tree was calculated from measurements of light interception or spectral reflectance (Table 1; Supplementary Fig. 1). Regression relationships between the relative deviation in growth from maximum, $(BAI_{90} - BAI)/BAI_{90}$, and both $LA_{90} - LA$ and $(LA_{90} - LA)/LA_{90}$ were weak (Table 1).

Possible stand-level and physiological predictors of growth

Sparsely foliated trees at Colorado Bend were more likely to be isolated than growing in woody patches, as $(LA_{90} - LA)/LA_{90}$ was negatively correlated with fractional interception of incident PAR by surrounding trees (Table 1). However, there was no significant correlation between growth deviation from maximum during the predrought period ($BAI_{90} - BAI$) for living trees and either PAR interception by surrounding trees ($P = 0.93$, $n = 45$) or soil depth (range 0.04–0.60 m) at Colorado Bend ($P = 0.49$, $n = 45$).

We also failed to find evidence that recent growth and LA of trees at Colorado Bend were closely linked to current physiological functioning. A resistance to water movement between leaves and stems of juniper was evident in more negative (lower) leaf than stem Ψ (Fig. 5).

The stem-to-leaf Ψ gradient was positively, albeit weakly, correlated to Ψ_{stem} in both 2014 and 2015 (Table 1), despite the greater variation in Ψ among trees (range = -2 to -8 MPa) and greater average water stress levels in 2015 than 2014. Provided that resistance to water transport was similar among trees, the positive link between the stem-to-leaf Ψ gradient and Ψ_{stem} implies that transpiration rate increased as Ψ_{stem} increased. PRI values were smaller on average for sunlit than bagged leaves at Colorado Bend (0.003 vs. 0.012 and 0.001 vs. 0.008, respectively, in 2014 and 2015; $n = 44$), as anticipated if light energy was being dissipated via nonphotochemical quenching. PRI of sunlit leaves, like the stem–leaf Ψ gradient, was a weak positive function of Ψ_{stem} (Table 1). However, there was no consistent relationship between the stem–leaf Ψ gradient or the PRI of sunlit leaves measured during periods of water limitation and deviation in either LA or growth from maximum for living trees (not shown; Ψ gradient, $P = 0.61$, 0.81 and 0.58 , 0.45 ; PRI, $P = 0.54$, 0.13 and 0.76 , 0.74 in 2014 and 2015, respectively; $n = 42$ – 44).

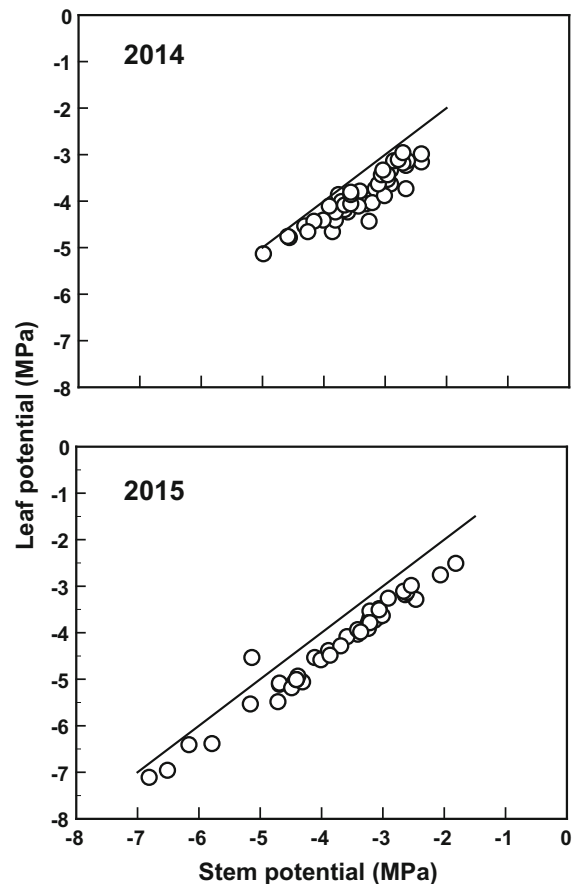


Fig. 5 Relationships between mid-day stem and leaf water potentials of juniper trees at Colorado Bend Park during summer dry periods in 2014 and 2015 ($n = 44$). The solid line illustrates the 1:1 relationship

Discussion

Slowly growing Ashe juniper trees were disproportionately vulnerable to mortality following the historic drought of 2011 in the Southern Plains. Drought killed $>85\%$ of trees for which predrought growth deviated by $>16\text{ cm}^2/\text{year}$ from ‘maximum’ values of predrought growth observed in the field for comparably sized trees ($BAI_{90} - BAI$). Mortality in our sample was confined to trees in the upper 60 % of the range defined by 23-fold variation in tree size. Of the variables measured, deviation in leaf area from maximum ($LA_{90} - LA$) was the strongest, readily measureable predictor of mortality of individual trees via its link with $BAI_{90} - BAI$. Together with residuals from a CA versus BA regression, $LA_{90} - LA$ explained as much as 55 % of the variance in

$BAI_{90} - BAI$. The relative deviation in LA from maximum $[(LA_{90} - LA)/LA_{90}]$ was greater among juniper individuals that were isolated than growing in proximity to other trees, but there was no significant correlation between $BAI_{90} - BAI$ for living trees and either the proximity of other trees, soil depth, leaf Ψ , the stem–leaf Ψ gradient, or an index of light use efficiency. Our data implicate size-standardized measurements of LA deviation from maximum as one key to rapidly and nondestructively estimating growth rate and mortality risk of Ashe juniper individuals.

Drought-caused mortality clearly was nonrandom, disproportionately befalling those individuals of Ashe juniper that grew most slowly during the decade prior to the drought event. Similar results have been reported for other tree species (Ogle et al. 2000; Suarez et al. 2005; Swaty et al. 2004). Slow growth is viewed as evidence for reduced vigor, the aggregate result of multiple, deleterious or ‘pre-disposing’ stressors, effects of which accumulate through time to heighten tree susceptibility to more acute stressors such as insect or pathogen infestations or climatic extremes (Manion 1981; Pedersen 1998). Our data are consistent with the apparent importance of cumulative, nonextreme plant stressors in increasing mortality risk. Ogle et al. (2000) also found that growth characteristics during the 10–15 years prior to drought predicted drought-induced death. Inter-annual variation in growth was 1.5 times greater among piñon (*Pinus edulis*) trees that died than survived.

Drought-caused mortality of juniper also was a nonlinear function of growth depression from maximum. Greater than 85 % of sampled trees died when BAI dipped by $16 \text{ cm}^2/\text{year}$ below BAI values for similarly sized trees growing on deep soil. By contrast, mortality was absent when BAI was $<16 \text{ cm}^2/\text{year}$ below maximum values. Results provide clear evidence of a threshold-like mortality response to the historic 2011 drought, wherein the death rate increased rapidly over a relatively narrow range in growth deviation from maximum.

Ashe juniper trees that grew slowly also had sparser canopies. Juniper experienced extreme negative Ψ as soil water was depleted. An obvious risk of such negative pressures is hydraulic failure, often accompanied by significant branch and canopy dieback (Pangle et al., 2015). Reduced LA of juniper thus may be a response to negative impacts of drought or other stressors on hydraulic conductance, essentially a mechanism to reestablish equilibrium between capacity for water transport and potential transpiration rates.

Downward adjustments in leaf area can enhance drought survival (Deines et al. 2011; Suarez et al. 2005). But, to the extent that canopy display parallels water transport capacity, sparse canopies signal hydraulic limitation which when sufficiently severe increases mortality risk. Carnicer et al. (2011), for example, observed a close association among water deficit, tree defoliation, and mortality rates in drier portions of woody species’ ranges. The ranking of mortality rates among three woody species in the Edwards Plateau region of Texas following the 2011 drought paralleled the ranking in sap flow decline among species measured during a previous drought (Kukowski et al. 2013).

Slow growth, as indicated by large $BAI_{90} - BAI$ values, also was positively correlated with residuals from a CA versus BA regression (Table 1). Slow growth thus was associated with greater than average values of CA for a given BA or conversely, smaller than average values of BA per unit of CA. For a given value of annual tree ring growth, calculated values of BAI increase proportionately with BA. Calculations of growth deviation from maximum thus are sensitive to relatively small variation in measured BA. Deviation in CA or BA values from those anticipated from the CA versus BA regression may result from true variation from an allometric relationship between the two variables, measurement error, or some combination of the two. Given the challenge of accurately measuring the diameter of the often irregularly shaped trunks of Ashe juniper, we suspect that measurement error contributed to deviation in CA or BA values from those anticipated from the CA versus BA regression relationship. We suggest that the BA used in calculating juniper BAI be estimated from measurements of CA, provided that the CA–BA relationship reported here is confirmed with additional data. Improving the reliability of BA estimates likely will strengthen the correlation between $BAI_{90} - BAI$ and $LA_{90} - LA$.

Several research groups have sought to identify functional, morphological, environmental, or other metrics of mortality risk from drought. Considerable progress has been made, but it remains difficult to predict the drought vulnerability of individual trees or of tree populations at local scales. Prediction remains a challenge because metrics of mortality risk often are based on general variables such as soil depth or texture, stand density, and past meteorological conditions (Bowker et al. 2012; Greenwood and Weisberg 2008; Gu et al. 2015; Twidwell et al. 2014), yielding

relationships that may differ among locations, or require intensive measurements, the results of which are not readily applied to calculating mortality risk among individuals (Breshears et al. 2009; Kukowski et al. 2013; Ogle et al. 2000; Pangle et al. 2015). For example, drought-caused mortality of mature Ashe juniper trees was greater in deep than shallow soils in semiarid savanna (Twidwell et al. 2014), but growth deviation from maximum was not related to soil depth in our study. Soil depth may be a poor predictor of water availability to trees in the fractured limestone soils we studied owing to the complexities of rooting behavior and water movement and storage in these soils (Schwinning 2008). Mortality risk is elevated among trees with chronically low hydraulic conductance (Heres et al. 2014; Pangle et al. 2015) or large inter-annual variation in tree ring widths (Ogle et al. 2000), but the intensive sampling required to quantify conductance and ring widths limits predictive capacity. Mortality risk of Ashe juniper individuals in the Edwards Plateau region can be estimated from non-destructive measurements of LA, CA, and BA using relationships among leaf area, tree growth, and mortality risk detailed above.

We find that heightened mortality risk is linked to slow growth (BAI) which, in turn, is linked to reduced LA in Ashe juniper trees. One limitation of using the risk-BAI-LA correlations developed here to predict drought vulnerability is asynchrony in measurements of growth and leaf display. BAI-mortality risk relationships were developed from predrought data. LA-BAI relationships were developed from postdrought data. Leaf area and projected canopy area (CA) change as trees grow. Leaf area, in particular, likely was reduced by drought, in our observations more through ‘leaf thinning’ than as a result of branch death as occurs in some species (Pangle et al. 2015). The LA-growth link is strongest when calculated from contemporary measurements of the two variables, as demonstrated in our data from the year 2012. Predictions of mortality risk thus might be improved by linking contemporary measurements of BAI deviation and LA deviation. Doing so would require that LAI and CA be measured on variously sized trees through time, perhaps annually or biennially. Tree cores would be required following the period of LAI and CA measurements to determine BAI. One then could calculate average values of LAI, CA (and hence, LA), and BAI for each tree over a period of years or, alternatively, extract values of these

variables for years in which annual precipitation approximated the long-term mean for each site. We anticipate that this approach would improve our capacity to estimate BAI deviation from LA deviation alone and thus to estimate mortality risk from the BAI-mortality relationship that was developed for a period with near-average precipitation.

Ashe juniper is a keystone species in the 93,000 km² Edwards Plateau region in west-central Texas, USA. Sparsely foliated juniper trees and those in which basal area is small compared to canopy area grow relatively slowly. Slowly growing trees are disproportionately vulnerable to mortality during drought. Given this linkage among leaf area, basal area, growth rate, and mortality, we recommend using measurements of tree leaf, canopy, and basal area, to estimate mortality risk of Ashe juniper individuals and ultimately, to predict fractional mortality risk of juniper populations at local to larger spatial scales.

Acknowledgments Field and laboratory assistance from Chris Kolodziejczyk, Katherine Jones, and Corey Courchane was critical. We are indebted to Texas Parks and Wildlife staff at Colorado Bend State Park for their gracious cooperation. This project was funded under a Grant from USDA-AFRI (#2012-00857). Mention of trade names or commercial products does not imply endorsement by the US Department of Agriculture. USDA is an equal opportunity provider and employer.

References

- Adams HD, Luce CH, Breshears DD, Allen CD, Weiler M, Hale VC, Smith AMS, Huxman TE (2012) Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses. *Ecohydrology* 5:145–159
- Allen CD, Breshears DD (1998) Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proc Natl Acad Sci USA* 95:14839–14842
- Begg JE, Turner NC (1970) Water potential gradients in field tobacco. *Plant Physiol* 46:343–346
- Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ (2015) Larger trees suffer most during drought in forests worldwide. *Nat Plants*. doi:10.1038/nplants.2015.139
- Bowker MA, Muñoz A, Martínez T, Lau KM (2012) Rare drought-induced mortality of juniper is enhanced by edaphic stressors and influenced by stand density. *J Arid Environ* 76:9–16
- Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, Allen CD, McDowell NG, Pockman WT (2009) Tree die-off in response to global change type drought: mortality insights from a decade of plant water potential measurements. *Front Ecol Environ* 7:185–189
- Cade BS, Noon BR (2003) A gentle introduction to quantile regression for ecologists. *Front Ecol Environ* 1:412–420

- Camarero JJ, Gazol A, Sangüesa-Barreda G, Oliva J, Vicente-Serrano SM (2015) To die or not to die: early warnings of tree dieback in response to severe drought. *J Ecol* 103:44–57
- Carnicer J, Coll M, Ninyerola M, Pons X, Sánchez G, Peñuelas J (2011) Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proc Natl Acad Sci USA* 108:1474–1478
- Deines JM, Hellmann JJ, Curran TJ (2011) Traits associated with drought survival in three Australian tropical rainforest seedlings. *Aust J Bot* 59:620–628
- Gamon JA, Serrano L, Surfus JS (1997) The photochemical reflectance index: an optical indicator of photosynthetic radiation use efficiency across species, functional types, and nutrient levels. *Oecologia* 112:492–501
- Greenwood DL, Weisberg PJ (2008) Density-dependent tree mortality in pinyon-juniper woodlands. *For Ecol Manag* 255:2120–2137
- Gu L, Pallardy SG, Hosman KP, Sun Y (2015) Drought-influenced mortality of tree species with different pre-dawn leaf water dynamics in a decade-long study of a central US forest. *Biogeosciences* 12:2831–2845
- Heres AM, Camarero JJ, López BC, Martínez-Vilalta J (2014) Declining hydraulic performances and low carbon investments in tree rings predate Scots pine drought-induced mortality. *Trees* 28:1737–1750
- Huang C, Asner GP, Barger NN, Neff JC, Floyd ML (2010) Regional aboveground live carbon losses due to drought-induced tree dieback in piñon-juniper ecosystems. *Remote Sens Environ* 114:1471–1479
- Intergovernmental Panel on Climate Change (2013) The physical science basis: contribution of Working Group I. Cambridge University Press, Cambridge
- Jiang X, Rauscher SA, Ringler TD, Lawrence DM, Williams AP, Allen CD, Stiner AL, Cai DM, McDowell NG (2013) Projected future changes in vegetation in western North America in the twenty-first century. *J Clim* 26:3671–3687
- Kukowski KR, Schwinning S, Schwartz BF (2013) Hydraulic responses to extreme drought conditions in three co-dominant tree species in shallow soil over bedrock. *Oecologia* 171:819–830
- Littell RS, Stroup WW, Freund RJ (2002) SAS for linear models, 4th edn. SAS Institute Inc, Cary
- Manion PD (1981) Tree disease concepts. Prentice Hall, Upper Saddle River
- Ogle K, Whitham TG, Cobb HS (2000) Tree-ring variation in pinyon predicts likelihood of death following severe drought. *Ecology* 81:3237–3243
- Pangle RE, Limousin J-M, Plaut JA, Yezpe EA, Hudson PJ, Boutz AL, Gehres N, Pockman WT, McDowell NG (2015) Prolonged experimental drought reduces plant hydraulic conductance and transpiration and increases mortality in a piñon-juniper woodland. *Ecol Evol* 5:1618–1638
- Pedersen BS (1998) The role of stress in the mortality of mid-western oaks as indicated by growth prior to death. *Ecology* 79:79–93
- Peng CH, Ma ZH, Lei XD, Zhu QA, Chen H, Wang WF, Liu SR, Li WZ, Fang XQ, Zhou XL (2011) A drought induced pervasive increase in tree mortality across Canada's boreal forests. *Nat Clim Change* 1:467–471
- Reidy JL, Thompson FR III, Schwoppe C, Rowin S, Mueller JM (2016) Effects of prescribed fire on fuels, vegetation, and Golden-cheeked warbler (*Setophaga chrysoparia*) demographics in Texas juniper-oak woodlands. *For Ecol Manag* 376:96–106
- Riskind DH, Diamond DD (1988) An introduction to environments and vegetation. In: Amos BB, Gehlbach FR (eds) Edwards Plateau vegetation: plant ecological studies in central Texas. Baylor Univ Press, Waco, pp 1–15
- Schwantes AM, Swenson JJ, Jackson RB (2016) Quantifying drought-induced tree mortality in the open canopy woods of central Texas. *Remote Sens Environ* 181:54–64
- Schwinning S (2008) The water relations of two evergreen tree species in a karst savanna. *Oecologia* 158:373–383
- Smeins FE, Merrill LB (1988) Long-term change in a semi-arid grassland. In: Amos BB, Gehlbach FR (eds) Edwards Plateau vegetation: plant ecological studies in central Texas. Baylor University Press, Waco, pp 101–114
- Suarez ML, Ghermandi L, Kitzberger T (2005) Factors predisposing episodic drought-induced tree mortality in Nothofagus: site, climatic sensitivity, and growth trends. *J Ecol* 92:954–966
- Swaty RL, Deckert RJ, Whitham TG, Gehring CA (2004) Ectomycorrhizal abundance and community composition shifts with drought: predictions from tree rings. *Ecology* 85:1072–1084
- Taucer PI, Munster CL, Wilcox BP, Owens MK, Mohanty BP (2008) Large-scale rainfall simulation experiments on juniper rangelands. *Trans ASABE* 51:1951–1961
- Twidwell D, Wonka CL, Taylor CA Jr, Zou CB, Twidwell JJ, Rogers WE (2014) Drought-induced woody plant mortality in an encroached semi-arid savanna depends on topographic factors and land management. *Appl Veg Sci* 17:42–52
- US Global Change Research Program (2009) Global climate change impacts in the United States. Karl TR, Melillo JM, Peterson TC (eds). Cambridge University Press, Cambridge. <http://www.globalchange.gov/usimpacts>. Accessed 10 Feb 2016
- van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fule PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH, Veblen TT (2009) Widespread increase of tree mortality rates in the western United States. *Science* 323:521–524
- Weiner J, Thomas SC (2001) The nature of tree growth and the “age-related decline in forest productivity”. *Oikos* 94:374–376
- Williams AP, Allen CD, Macalady AK, Griffin D, Woodhouse CA, Meko DM, Swetnam TW, Rauscher SA, Seager R, Grissino-Mayer HD, Dean JS, Cook ER, Gangodagamage C, Cai M, McDowell NG (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat Clim Change* 3:292–297
- Wold S, Ruhe A, Wold H, Dunn WJ III (1984) The collinearity problem in linear regression. The partial least squares (PLS) approach to generalized inverses. *SIAM J Sci Stat Comput* 5:735–743
- Zou CB, Turton DJ, Will RE, Engle DM, Fuhlendorf SD (2014) Alteration of hydrological processes and streamflow with juniper (*Juniperus virginiana*) encroachment in a mesic grassland catchment. *Hydrol Process* 28:6173–6182