

Growth, carbon-isotope discrimination, and drought-associated mortality across a *Pinus ponderosa* elevational transect

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Abstract

Drought- and insect-associated tree mortality at low-elevation ecotones is a widespread phenomenon but the underlying mechanisms are uncertain. Enhanced growth sensitivity to climate is widely observed among trees that die, indicating that a predisposing physiological mechanism(s) underlies tree mortality. We tested three, linked hypotheses regarding mortality using a ponderosa pine (*Pinus ponderosa*) elevation transect that experienced low-elevation mortality following prolonged drought. The hypotheses were: (1) mortality was associated with greater growth sensitivity to climate, (2) mortality was associated with greater sensitivity of gas exchange to climate, and (3) growth and gas exchange were correlated. Support for all three hypotheses would indicate that mortality results at least in part from gas exchange constraints. We assessed growth using basal area increment normalized by tree basal area [basal area increment (BAI)/basal area (BA)] to account for differences in tree size. Whole-crown gas exchange was indexed via estimates of the CO₂ partial pressure difference between leaf and atmosphere ($p_a - p_c$) derived from tree ring carbon isotope ratios ($\delta^{13}\text{C}$), corrected for temporal trends in atmospheric CO₂ and $\delta^{13}\text{C}$ and elevation trends in pressure. Trees that survived the drought exhibited strong correlations among and between BAI, BAI/BA, $p_a - p_c$, and climate. In contrast, trees that died exhibited greater growth sensitivity to climate than trees that survived, no sensitivity of $p_a - p_c$ to climate, and a steep relationship between $p_a - p_c$ and BAI/BA. The $p_a - p_c$ results are consistent with predictions from a theoretical hydraulic model, suggesting trees that died had a limited buffer between mean water availability during their lifespan and water availability during drought – i.e., chronic water stress. It appears that chronic water stress predisposed low-elevation trees to mortality during drought via constrained gas exchange. Continued intensification of drought in mid-latitude regions may drive increased mortality and ecotone shifts in temperate forests and woodlands.

Keywords: altitude, climate change, die-off, photosynthesis, stomatal conductance, water availability

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Introduction

Drought-induced vegetation mortality has rapid, widespread and long-lasting impacts on the biotic composition of landscapes (Allen & Breshears, 1998; Berg *et al.*, 2006). Mortality-driven changes in ecosystem structure

and function can result in ecotone shifts (Allen & Breshears, 1998), altered wildfire hazard and increased erosion (Allen, 2007), decreased carbon storage (Breshears & Allen, 2002; Kurz *et al.*, 2008), and shifts in surface hydrology (Newman *et al.*, 2006). Recent drought-related forest mortality has been observed throughout the world (e.g. Condit *et al.*, 1995; Swetnam & Betancourt, 1998; Fensham & Holman, 1999; Gonzalez, 2001; Suarez *et al.*, 2004; Bigler *et al.*, 2006; van Mantgem & Stephenson, 2007; McDowell *et al.*, 2008a,

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Raffa *et al.*, 2008; Fensham *et al.*, 2009; Allen, 2009) and may be associated with increased surface temperatures (Breshears *et al.*, 2005; van Mantgem *et al.*, 2009). This mortality is occurring despite the sometimes observed CO₂ fertilization of tree growth (Tang *et al.*, 1999; Martínez-Vilalta *et al.*, 2008) and water use efficiency (Saurer *et al.*, 2004; Peñuelas *et al.*, 2008). Climate-associated mortality is exemplified in western North America, where widespread mortality of dominant species, such as most members of the *Pinaceae*, has recently been observed throughout the length of the Rocky Mountains (Raffa *et al.*, 2008). Climate-induced vegetation mortality is a growing global concern (Allen & Breshears, 2007) due to the projections of increasing drought severity and frequency in many regions of the world (Lawford *et al.*, 1993; Hanson & Weltzin, 2000; Rosenberg *et al.*, 2003; Weltzin *et al.*, 2003; Cook *et al.*, 2004; McCabe *et al.*, 2004; IPCC, 2007; Seager *et al.*, 2007).

There is currently no consistent mechanism identified to explain why trees die during drought and associated pathogen outbreaks (e.g. bark beetle, *Ips* Raffa *et al.*, 2008; Bentz *et al.*, 2009), but the general consensus is that mortality depends in part on the whole tree carbon budget (e.g. Manion, 1981; Waring, 1987; McDowell *et al.*, 2008a). This is reflected in empirical observations that consistently show greater sensitivity of stemwood growth to climate in trees that die compared with those that survive (Pedersen, 1998; Demchik & Sharpe, 2000; Ogle *et al.*, 2000; Suarez *et al.*, 2004). Greater growth sensitivity to climate, i.e. steeper slopes of a regression of growth versus climate, has also been seen in trees from low elevation ecotones in comparison with higher elevation locations (Adams & Kolb, 2004; Peñuelas *et al.*, 2008), and lower elevation ecotones typically experience greater mortality (Allen & Breshears, 1998). This common observation may be explained by the logical cascade of events in trees that die, from water stress to particularly reduced photosynthesis and subsequently reduced growth and production of resin to fend off insect attack (Gaylord *et al.*, 2007).

For isohydric species that maintain relatively constant mid-day leaf water potential regardless of soil moisture variability, a potential mechanism is that mortality occurs due to the avoidance of hydraulic failure via stomatal closure, which results in carbon starvation and subsequent susceptibility to biotic attack (McDowell *et al.*, 2008a). Stomatal closure during drought constrains carbon uptake because of the dependence of photosynthetic assimilation (A) on conductance (g) (Farquhar *et al.*, 1980):

$$A \approx g(c_a - c_c). \quad (1)$$

In this representation of Fick's law, c_a and c_c are atmospheric and chloroplast CO₂ concentrations and g

represents stomatal (g_s) and mesophyll conductance (g_m). It is well established that g_s is curtailed during dry periods to minimize hydraulic failure (Sperry *et al.*, 2002), and therefore periods of extreme drought can conceivably result in little or no photosynthesis (Gaylord *et al.*, 2007; McDowell *et al.*, 2008a). Extended periods without photosynthesis may cause mortality because, while carbon allocation to wood growth may cease temporarily without death, carbon allocation to maintenance respiration (Ryan *et al.*, 1995; Amthor, 2000) must continue at some basal level or mortality is inevitable (Marshall & Waring, 1985). Likewise, defense against insect attack requires sufficient carbon reserves to generate defensive compounds and sufficient phloem pressure to occlude insect entry holes (Coley *et al.*, 1985; Cobb *et al.*, 1997; Wallin *et al.*, 2003; McDowell *et al.*, 2007). Therefore, to the extent that wood growth is correlated with photosynthesis (e.g. Waring *et al.*, 1998; Litton *et al.*, 2007) and with resin flow (McDowell *et al.*, 2007), it is logical to expect that wood growth is an indicator of tree predisposition to mortality. This hypothesis is consistent with theoretical, empirical, and model-based mortality research (reviewed in McDowell *et al.*, 2008a).

Two tools that have proven useful for investigations of climate constraints on growth are (1) elevation transects as a study design and (2) stable carbon isotope ratios ($\delta^{13}\text{C}$) as an index of gas exchange. Elevation transects allow understanding of growth constraints associated with climate (e.g. Lajtha & Getz, 1993; Adams & Kolb, 2004) and ecotone dynamics (Gitlin *et al.*, 2006; Beckage *et al.*, 2008; Kelly & Goulden, 2008) because temperatures are generally cooler and moisture availability greater with increasing elevation (Körner, 2007) and because lower elevation ecotones are typically dynamic in response to moisture stress (Allen & Breshears, 1998). The $\delta^{13}\text{C}$ of plant material has frequently been used as an index of gas exchange because it is dependent on the balance of CO₂ diffusion into and out of the chloroplast, which results from photosynthesis and g [Eqn (1), see 'Materials and methods' for further description, Seibt *et al.*, 2008]. Tree-ring $\delta^{13}\text{C}$ is particularly useful because it provides a whole-crown, assimilation weighted record of gas exchange that can be discretized to individual years, allowing analyses of the response of individual trees to climatic variation (Francey & Farquhar, 1982; Walcroft *et al.*, 1997; Pate, 2001). There is a long tradition of combining $\delta^{13}\text{C}$ analyses with elevation transects (e.g. Vitousek *et al.*, 1990; Körner *et al.*, 1991; Marshall & Zhang, 1994; Sparks & Ehleringer, 1997; Cordell *et al.*, 1999; Hultine & Marshall, 2000; Warren *et al.*, 2001; Van de Water *et al.*, 2002; Adams & Kolb, 2004; Peñuelas *et al.*, 2008), though no prior studies

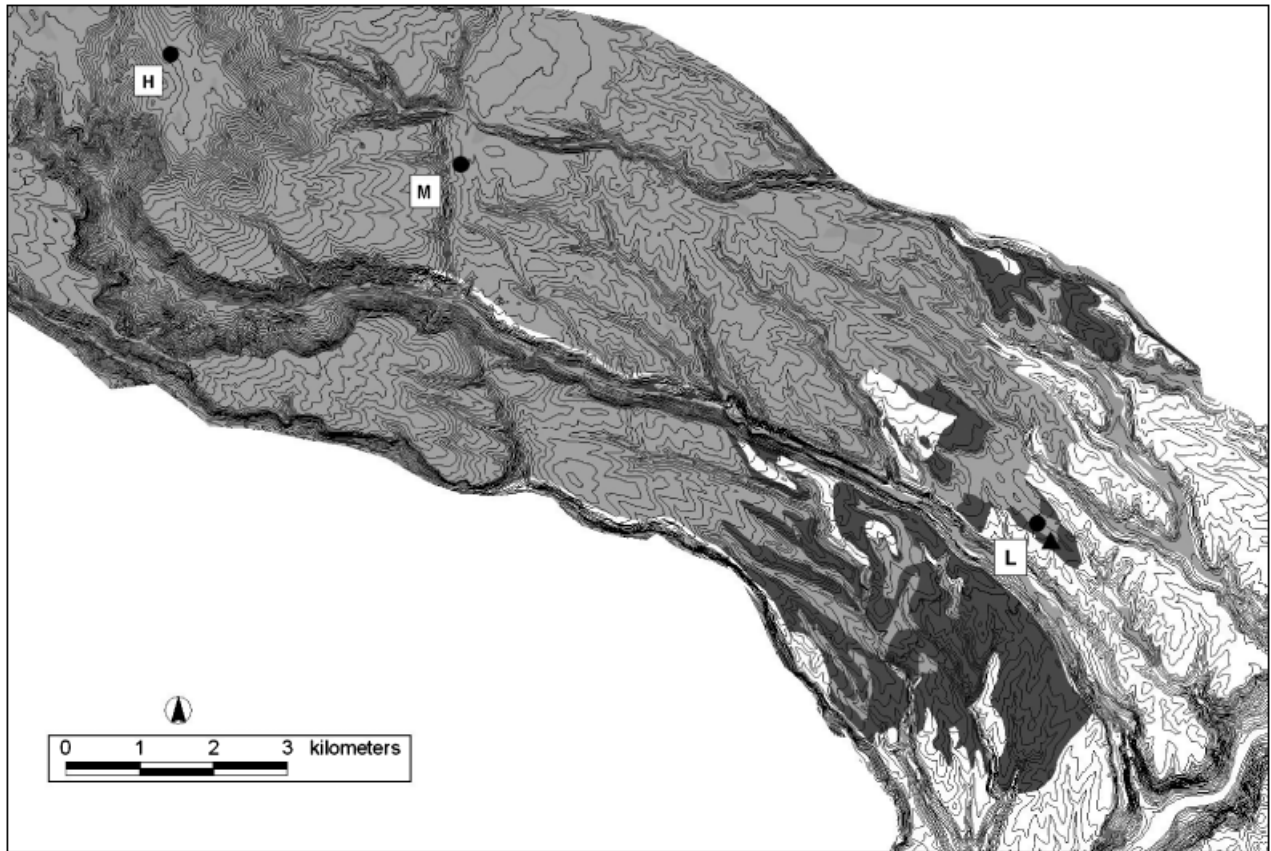


Fig. 1 Locations of High (H), Mid (M), and Low (L) live (circle) and dead (triangle) sites along an elevation gradient in Bandelier National Monument, 12.2 m (40 ft) contours displayed. Shading indicates persistent forest (light gray), persistent woodland (white), and ponderosa forest mortality zone (dark gray) from a previous severe drought in the 1950s (mapped by Allen, 1989; Allen & Breshears, 1998), showing that the Low site is located at the 2002 forest/woodland ecotone. Extensive low-elevation ponderosa pine mortality in 2002–2003 caused this ecotone to shift further upslope (unmapped).

have used these tools to investigate mechanisms of mortality.

Additional tools available to interpret empirical results regarding climatic sensitivity of gas exchange are simple theoretical models of plant hydraulics. The impact of atmospheric and soil water content on gas exchange can be approximately predicted by a hydraulic corollary to Darcy's Law applied to trees (Whitehead *et al.*, 1984):

$$g_s = \frac{k_1(\Psi_s - \Psi_l)}{VPD}, \quad (2)$$

in which k_1 is whole plant hydraulic conductance, Ψ_s is soil water potential (MPa), Ψ_l is daytime leaf water potential, and VPD is vapor pressure deficit (VPD, kPa). Manipulating VPD and Ψ_s in Eqn (2) allows one to predict the response of g_s (and A) to drought. More complex versions of this model exist (e.g. Whitehead, 1998; Oren *et al.*, 1999; Phillips *et al.*, 2002), and more complex hydraulic models exist (e.g. Williams *et al.*,

2001; Sperry *et al.*, 2002); however, the simple framework in Eqn (2) allows interpretation of gross level impacts of chronic differences in Ψ_s and VPD on whole-tree gas exchange in the absence of detailed parameterization data (McDowell *et al.*, 2005, 2008b).

The objective of our study was to quantify annual patterns of ponderosa pine (*Pinus ponderosa*) growth and $\delta^{13}C$ in relation to climate along an elevation gradient (Fig. 1). The lower ecotone of this gradient experienced widespread mortality following a recent multi-year drought (Fig. 2) whereas the forests at the middle and upper elevations largely survived. As such, we sampled both live and recently dead trees (2002–2004) at the lower ecotone for comparison with live trees at the middle and upper elevations. This experimental design allowed us to test hypotheses regarding tree mortality both within a site and across the elevation transect. We tested three hypotheses: (1) mortality was associated with greater growth sensitivity to climate, (2) mortality was associated with greater sensitivity of gas

exchange to climate, and (3) variation in growth was correlated with gas exchange. Hypotheses (1) and (3) were tested empirically using tree ring growth and $\delta^{13}\text{C}$, and hypothesis (2) was tested both empirically and theoretically with the Whitehead model, in which the model was employed to assess gas exchange patterns in trees that survived and died. Confirmation of



Fig. 2 Low-elevation ponderosa pine trees that died in 2002–2003 near the Low site. The surviving understory of *Juniperus monosperma* is typical of transition to woodland at such lower ecotone sites.

these three hypotheses would support the idea that the mechanism of mortality was related to gas exchange constraints on photosynthesis.

Materials and methods

Study sites

Ponderosa pine is a widespread conifer in North America, occurring from central Mexico to southern Canada (Waring & Law, 2001) and is an economically important species in both public and private forests. This species is expected to undergo widespread mortality in the 21st century in response to climate change (Coops *et al.*, 2005). Our study was conducted in three stands of ponderosa pine situated along a 750 m elevation transect across 15 km within Bandelier National Monument (Fig. 1), located in the Jemez Mountains of northern New Mexico (Table 1). The soil parent materials at all three sites are volcanic in origin, ranging from rhyolite to tuff with some pumice components. Soils are Alfisols on level to gentle terrain at all three sites, with more pumice-linked Mollisol elements at mid and low elevation sites (NRCS, 2007). Dominant vegetation varies along the elevation gradient. The low-elevation site contains multiple age classes (up to 300 years) of ponderosa pine in an open stand mixed with an understory of piñon (*Pinus edulis*) and juniper (*Juniperus monosperma*, Fig. 2). The mid-elevation site is a denser, close-canopied stand of largely even-aged (ca. 95 years) ponderosa pine. The high-elevation site contains multi-aged (up to ~180 years) ponderosa pine mixed with Douglas-fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*). Far less mortality occurred at the middle or high elevation sites. At all sites, the sampled trees were canopy dominants with minimal crown shading from neighboring trees. More site details can be found in

Table 1 Site characteristics including coordinates (latitude and longitude), elevation (m), stand density (live and dead, all species, all sizes) as # of trees per hectare and as basal area ($\text{m}^2 \text{ha}^{-1}$), and mean annual climate for the study period (1992–2002) including precipitation (mm), maximum and minimum temperature ($^{\circ}\text{C}$) and vapor pressure deficit (kPa) during daylight hours

Site	Low	Mid	High
Coordinates	35°79'N 106°27'W	35°84'N 106°40'W	35°84'N 106°36'W
Elevation (m)	2000	2310	2750
Density (# ha^{-1})	165 (19)	587 (62)	430 (57)
Basal area ($\text{m}^2 \text{ha}^{-1}$)	8.8 (1.3)	32.1 (2.2)	29.2 (3.1)
Annual Precipitation (mm)	350 (23)	440 (30)	500 (31)
Maximum Temperature ($^{\circ}\text{C}$)	18.2 (0.2)	15.7 (0.2)	9.5 (0.2)
Minimum Temperature ($^{\circ}\text{C}$)	1.2 (0.1)	2.3 (0.2)	0.0 (0.25)
VPD (kPa)	1.6 (0.03)	1.3 (0.03)	0.75 (0.02)

Values in parentheses are SE of the 11 year means.

Table 1. For the remainder of the paper we refer to the three sites as Low, Mid, and High, respectively.

This region experiences a monsoonal climate typical of the southwestern U.S., with precipitation distributed in a bimodal pattern with peaks in the winter (November–March) and summer monsoon (July–early September), with a pronounced drought during May and June. There are clear elevation trends in dominant climatic characteristics between sites (Table 1).

Experimental design and statistics

This study was originally designed in 1991 to provide information on elevation patterns of growth in relation to climate, with dendrometer bands placed on 10 target trees at each of three distinct elevation sites. Trees were originally selected to capture both dominant and co-dominant canopy classes at each site. The Low site was established at the lowest-elevation fringe of ponderosa pine in this landscape in 1991. There was 100% mortality of the dendrometer banded trees at the Low site in 2002–2003 (Figs 1 and 2), whereas all Mid and High site trees survived. Although this outcome was not predictable *a priori*, it confounds elevation and mortality for this study. We took advantage of this added complexity by sampling an equal number of Low site trees that survived the drought along with the original dendro-banded trees that died. We selected the nearest possible live trees to the sampled dead trees, which were typically within 100 m distance. This sampling design allows a direct test of our hypotheses between trees that survived and died at the Low site, as well as comparison of trees that died and survived at the Low site to trees that survived at higher elevations.

To test the hypothesis that mortality was associated with greater growth sensitivity to climate, we compared slopes of growth vs. climate parameters via analyses of covariance, and analysis of variance to compare inter-annual variability in growth within and between sites. We also calculated the ratio of growth for wet vs. dry years (W:D, Adams & Kolb, 2004) and used analyses of variance to test for W:D differences within and between sites. Palmer drought severity index (PDSI) was used as an index for characterization of wet and dry years. PDSI is a measure of meteorological drought calculated from precipitation, temperature and potential evapotranspiration, with more negative values indicative of drought (Palmer, 1965). The five wettest years, based on PDSI, were 1992–1995 and 1999, and driest years were 1996, 1998, and 2000–2002. We used linear regression to test the hypothesis that variation in growth was associated with $\delta^{13}\text{C}$ -based estimates of Δ and p_a p_c (described under the 'Materials and methods' section on carbon isotopes). Analysis of variance

was used for all other analyses of differences between elevations such as for leaf nitrogen and specific leaf area. For the purpose of avoiding confounding and making more complex our hypothesis tests, we did not assess autocorrelation because it varies with elevation and is typically nonexistent for low elevation trees in southwestern USA (C. Baisan, personal communication). All statistical analyses were conducted with SYSTAT 11.0 (Systat, 2004).

Growth

Dendrometer bands were established on thirty ponderosa pine trees, 10 per site, in June 1991, with manual recording of circumference changes (0.1 mm resolution) on approximately a weekly schedule during April–October, and bi-monthly during the winter. Basal area increment (BAI, $\text{cm}^2 \text{yr}^{-1}$) was calculated from weekly stem circumference measurements made from 1992 (the first full year of growth data) through autumn 2002 (when tree mortality occurred at the Low site). Ring widths were converted to BAI from 1992 to 2002 using tree-specific circumferential growth (inside bark) and assuming concentric circularity. There were a different number of measurements each year, precluding inter-annual analyses by day of year. Thus for inter-annual comparison of temporal dynamics of responses to drought we calculated site/week means and normalized them to 365 days, i.e. $\text{day } X/365$.

For live trees at the Low site, BAI was calculated from breast height diameter (corrected for bark and phloem widths) and ring width measurements (McDowell *et al.*, 2006, and below) because they were not recorded with dendrobands during the period of this study. Comparison of BAI calculated via dendroband and via microscope ring width measurements for the Low dead trees revealed no detectable bias between methods (slope 1.01, $R^2 = 0.96$, data not shown). BAI was normalized by basal area (BAI/BA, $\text{cm}^2 \text{cm}^{-2} \text{yr}^{-1}$) to account for the inherent differences in tree size associated with differences in elevation-related productivity and tree age, allowing us to more precisely examine their relative drought responses. Temporal patterns and regression slopes are similar for either BAI or BAI/BA so for simplicity and accuracy, only BAI/BA is shown (after Fig. 3).

Carbon isotope composition

Photosynthesis by ponderosa pine discriminates against ^{13}C relative to ^{12}C because ^{13}C has a lower diffusivity through the stomatal pore and lower reactivity with the photosynthetic enzyme ribulose 1,5 bisphosphate carboxylase-oxygenase. This

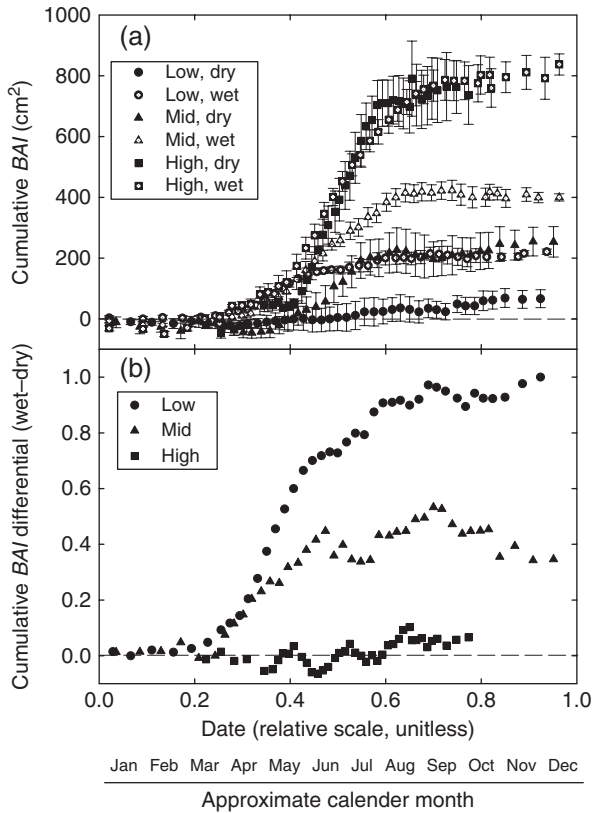


Fig. 3 (a) Weekly basal area increment for the Low (dead), Mid, and High sites, averaged for the five wet and five dry years (see 'Materials and methods' for years of averaging). Calendar months are provided for reference. Scale bars are standard errors. (b) The relative growth differential for each site, calculated as: (mean BAI wet - mean BAI dry) / maximum BAI.

discrimination (Δ) results in $\delta^{13}\text{C}$ of the carbon within ponderosa pine tree rings to be approximately 15–25‰ below that of atmospheric CO_2 . Discrimination can be expressed relative to c_c/c_a (Farquhar *et al.*, 1989):

$$\Delta = a + (b - a) \frac{c_c}{c_a}, \quad (3)$$

where a is the fractionation associated with diffusion in air (4.4‰), b is the net fractionation associated with carboxylation by Rubisco (27–29‰), and c_a and c_c are as described for Eqn (1) [note that c_c is often written as internal CO_2 or c_i but we are using c_c to be consistent with Eqn (1)]. While Δ is a useful parameter, in elevation studies it is confounded with atmospheric pressure and therefore a final correction for shifts in the partial pressure of CO_2 must be made, which converts concentrations (c_a and c_c) to partial pressures (p_a and p_c ; Hultine & Marshall, 2000). Gas exchange parameters such as intrinsic water use efficiency (A/g , Ehleringer

et al., 1993) can be assessed using Δ estimates and Eqns (1) and (3).

In March 2004, we collected 12 mm diameter increment cores from five of the dendrometer banded trees at each plot. We additionally sampled cores from five live trees at the Low site in July 2007 to allow the within-site comparison of dead and live trees. Cores were removed from each tree at 1.3 m height. Cores were subsequently air dried for 2–3 months before further analysis. We sanded the cores using successively finer sandpaper of FEPA (Fed. of European Producers of Abrasives) 100, 220, and 320 grit (162, 68, and 44.7–47.7 μm , respectively, Orvis & Grissino-Mayer, 2002). When necessary we also used FEPA 400 grit sandpaper (33.5–36.5 μm , Orvis & Grissino-Mayer, 2002). Cores were cross dated visually using narrow marker years from tree-ring chronologies collected at local sites for ponderosa pine (*C. Baisan*, personal communication). In all instances the outer ring date was known, being the collection year for the living trees sampled and from monitoring of the mortality at the Low site. Each ring was precisely cross-dated to its year of formation, using standard dendrochronological methods (Stokes & Smiley, 1968). The sample size was five trees per year and per elevation for $\delta^{13}\text{C}$ measurements with the exception of the dead trees at the Low site, which had only four samples in 2002 due to missing rings.

After the increment cores had been cross-dated we split annual rings from each core using a scalpel and a dissecting scope. We did not attempt to separate early- from late-wood (Livingston & Spittlehouse, 1996; Leavitt & Wright, 2002) because our objective was to examine crown-scale gas exchange at the annual time step. We did not extract cellulose before measurement of $\delta^{13}\text{C}$ because numerous studies have reported constant relationships between cellulose and whole-wood $\delta^{13}\text{C}$ for sapwood (Livingston & Spittlehouse, 1996; Marshall & Monserud, 1996; Macfarlane *et al.*, 1999; Warren *et al.*, 2001; Loader *et al.*, 2003; Harlow *et al.*, 2006), and most cross-ring contamination is associated with carbon movement from the sapwood into the heartwood (S. Leavitt, personal communication) and all of our sample rings were located within the sapwood. Each ring was individually diced and ground to a fine powder using a mortar and pestle. The powder collected from each ring was analyzed on a Eurovector Elemental Analyzer coupled to an Isoprime isotope ratio mass spectrometer (GV Instruments, Manchester, UK) operated in continuous flow mode at Los Alamos National Laboratory's Stable Isotope Lab in Los Alamos, NM, USA. Nitrous oxide was removed by gas chromatography and corrections for ^{17}O (Craig, 1957) were done for all runs. We ran 208 tree ring samples and overall precision for $\delta^{13}\text{C}$ was 0.05‰ ($n = 52$).

Table 2 Coefficients of determination (r^2) for regressions between climate, p_a p_c and BAI

Parameter	Low-dead		Low-live		Mid		High	
	p_a p_c	BAI/BA	p_a p_c	BAI/BA	p_a p_c	BAI/BA	p_a p_c	BAI/BA
Min R_h	0.00	0.85	0.51	0.59	0.70	0.93	0.95	0.57
VPD	0.01	0.84	0.63	0.75	0.74	0.94	0.95	0.53
Precipitation	0.00	0.39	0.01	0.13	0.69	0.75	0.88	0.53
Min T_a	0.09	0.31	0.27	0.34	0.63	0.60	0.74	0.43
Max T_a	0.01	0.76	0.56	0.74	0.74	0.89	0.88	0.45
PDSI	0.00	0.86	0.48	0.87	0.73	0.85	0.84	0.48
Average	0.02	0.67	0.41	0.57	0.71	0.83	0.86	0.50

The regressions were conducted to assess the impact of using climate means from different time periods when examining climatic sensitivity. Time periods analyzed included previous winter, May–August, March–September, April–July, and annual means, but the best fits were found for March–September so only those are shown to save space. The coefficients for BAI and BAI/BA were within 0.02 of each other on average, so we present only the results for BAI/BA. Parameters are defined in the ‘Materials and methods’. Significant correlations at $\alpha = 0.05$ are bolded.

Tree ring $\delta^{13}C$ was converted to Δ (Farquhar *et al.*, 1982):

$$\Delta = \frac{\delta^{13}C_a - \delta^{13}C}{1 + \delta^{13}C} \quad (4)$$

We obtained annual atmospheric stable carbon isotope ratios ($\delta^{13}C_a$) from the Institute for Arctic and Alpine Research (INSTAAR) at the University of Colorado and the National Oceanic and Atmospheric Administration (NOAA), Earth System Research Laboratory (ESRL). Equation (4) corrects for annual depletion of $\delta^{13}C_a$ associated with fossil fuel emissions of CO_2 depleted in $\delta^{13}C$ (Leavitt & Long, 1988; Keeling *et al.*, 1989).

We calculated the partial pressure of CO_2 at the leaf surface (p_a) and within the chloroplast (p_c) using the method of Hultine & Marshall (2000) to correct for elevation differences in atmospheric pressure (Körner, 2007). We used mean CO_2 concentration data from NOAA-ESRL and elevation specific maximum air temperature averaged for the months of April–September for each individual year (1992–2002), and calculated c_c from Eqn (3). We then calculated the drawdown of CO_2 between the atmosphere and the chloroplast ($p_a - p_c$) because this results from the balance of CO_2 uptake by photosynthesis and stomatal conductance to CO_2 and constitutes the numerator in water use efficiency calculations (Marshall & Zhang, 1994; Hultine & Marshall, 2000). We examined both Δ and p_a p_c for both between and within site analyses. The results of regressions of both Δ and p_a p_c vs. climate and growth were similar, so we present primarily p_a p_c results because this parameter accounts for the elevation-driven changes in barometric pressure.

We were concerned about cross-contamination of $\delta^{13}C$ between rings during the process of splitting the

cores from trees at the Low site due to their particularly small rings. We conducted a sensitivity analyses in which we regressed Δ vs. climate variables (those shown in Table 2) the following ways: (1) re-arrangement of Δ values for neighboring rings (e.g., swapping 1998 Δ with 1999 Δ) – this represents the most likely way contamination could occur; (2) using only Δ values for 1992–1999, the years before the particularly severe drought with the particularly small rings; and (3) #2 repeated without cores that we noted had particularly small rings. This analysis failed to generate any significant relationships (best r^2 and P -value were 0.09 and 0.31, respectively). In addition to this analysis, visual examination of the Δ results confirms that even if carbon contaminated across rings, there is no ring that has Δ values sufficiently negative to provide a significant regression of Δ or p_a p_c vs. climate. We conclude that the $\delta^{13}C$ values for dead and live trees at the Low site are accurate, though signal attenuation remains a concern.

Leaf nitrogen and specific leaf area

Photosynthetic capacity and mesophyll conductance can affect $\delta^{13}C$ interpretation because they can alter p_c without variation in g_s . Leaf nitrogen concentration (N , %) and specific leaf area (SLA, $cm^2 g^{-1}$), respectively, are commonly used metrics of these factors (e.g. Evans, 1989; Evans *et al.*, 1994; respectively, but see Warren *et al.*, 2003), and may vary with elevation. It is currently impossible to quantify leaf N or SLA retrospectively through tree rings (e.g. Hart & Classen, 2003), so we sampled foliage from trees at each site in June 2006 and assumed that N and SLA from this date were representative of the relative differences between sites. We sampled foliage from the south aspect of the upper

crown third of each tree using an extendable pole pruner. Because all of the dendrometer-banded trees used for BAI and $\delta^{13}\text{C}$ at the Low site died in 2002, the only foliage samples from this site are from the live trees. For the Mid and High sites we sampled the original dendrometer banded trees. All sampling was done on the same day, and foliage was immediately returned to our laboratory, stored in plastic bags in a refrigerator and measured the next day for leaf area. Projected leaf area was determined using a LI-3100 Leaf Area Meter (Li-Cor, Lincoln, NE, USA) calibrated to 0.01 cm^2 (McDowell *et al.*, 2008b). The foliage was then dried at 65°C until the weight had stabilized to calculate the dry weight for *SLA*. Each foliage sample was ground to a fine powder using a mortar and pestle, and leaf *N* was measured on a Vario Max CN macro elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany).

Climatic response

To test our hypothesis regarding climatic sensitivity we examined relationships between BAI, BAI/BA, Δ , and $p_a - p_c$ with PDSI. We used instrumental PDSI data for Climate Division 2 (northern mountains) of New Mexico, available from the National Climatic Data Center (<http://www.ncdc.noaa.gov>). PDSI was used as the independent variable in regression analysis. Our study period of 1992–2002 occurred at the transition from an ~ 20 year wet period experienced by the region (1978–1995) into a dry period (post-1995). The years considered severe ‘drought’ years locally are 1996, 1998, 2000, 2001, and 2002. Wood growth in ponderosa pine occurs during the spring and summer months, so in order to ensure that we were using PDSI from the appropriate time period we conducted a correlation analyses of Δ , $p_a - p_c$, BAI, and BAI/BA vs. PDSI from different time periods, including annual means, means of the previous winter (October–March), and means of different periods during the spring and summer. The strength of regressions did not exhibit a consistent dependency on which ‘growing season’ period was used. For all subsequent analyses of climate vs. growth, Δ and $p_a - p_c$ we use the March–September time period because this period had slightly higher coefficients of determination and because this time period encompasses the period of growth based on dendrometer band measurements (Fig. 3). There were no significant differences between regressions using BAI and BAI/BA, or using Δ and $p_a - p_c$, so Table 2 and subsequent figures show only regressions using BAI/BA and $p_a - p_c$.

Our PDSI values are specific to our study region but are not calculated for each specific elevation. Therefore, we also conducted correlation analyses using climate

data from the nearest meteorological stations to our specific sites. The three sites are located at 1996, 2263, and 3157 m in elevation, and are within 1, 5, and 5 km of each of our study sites, respectively. These sites are maintained by Bandelier National Monument and the Los Alamos National Laboratory Meteorology Team (www.weather.lanl.gov). Climate characteristics including relative humidity (R_h , %), VPD (kPa), precipitation (mm), air temperature (T_a , $^\circ\text{C}$), and PDSI were used (Table 2).

The hydraulic model

We applied Eqn (2) in a similar fashion to Oren *et al.* (1999) and McDowell *et al.* (2005, 2008b). Only VPD, Ψ_s , and k_1 were allowed to vary in this modeling exercise. We used growing season (April–September), elevation-specific VPD for the 11 years of this study (1992–2002). We calculated Ψ_s as a relative function of elevation-specific precipitation during the growing season. This is accomplished by dividing the maximum, elevation-specific annual precipitation by each year’s total precipitation. This resulted in values for Ψ_s , Ψ_1 ranging between 0.35 (lowest precipitation) and 1.0 (highest precipitation) for each site. We assumed that Ψ_1 is constant (isohydric) regardless of site water availability (Maherali & Delucia, 2001) and that k_1 is highest at the Low site (set to 1.0) and decreased 10% between each successive higher elevation site (0.9 and 0.8 at the Mid and High sites, Maherali & Delucia, 2001). We allowed k_1 to decline with drought at variable rates for each site (Maherali *et al.*, 2002); however, this did not significantly alter the results so for simplicity we only present the results with k_1 constant over time. To examine the role of k_1 in tree mortality, we varied k_1 in 0.01 increments for the dead trees and examined the fit of the regression of modeled g_s vs. observed $p_a - p_c$ (the regression included all sites). The rationale for this analysis stemmed from our absolute lack of knowledge of k_1 in dead trees and because k_1 integrates many hydraulic parameters (e.g. leaf area:sapwood area ratio, rooting depth, sapwood permeability) that may vary between live and dead trees.

Results

Climate

A summary of climate characteristics for the elevation-specific meteorological stations during the study period of 1992–2002 is shown in Table 1. The Low, Mid, and High elevation sites exhibited the expected differences in climate, with the Low site being the warmest and driest and the High site the coolest and wettest. All

comparisons in Table 1 had significant differences between elevations ($P < 0.05$) except basal area between Mid and High ($P = 0.21$).

Intra-annual growth

Figure 3a shows weekly cumulative BAI averaged for the five wettest years and five driest years. Figure 3b shows the relative growth differential calculated as: (mean BAI wet–mean BAI dry)/maximum BAI, which is an index of the response of BAI to climate. Growth started in mid-April for the High and Mid sites for both wet and dry years (Fig. 3a). Growth at the Low site preceded the High and Mid sites by 1 or 2 weeks in wet years. Low site growth was delayed until early July in dry years, though pin scar measurements indicate cell division occurred in April and went undetected by dendrometer bands, perhaps due to dehydration-induced stem shrinkage (Allen *et al.*, 2009). Growth ended 1 or 2 weeks earlier in dry years than wet years, and ended earlier at lower elevations. The climatic dependency of growth clearly increased as site elevation decreased (Fig. 3b). Note that High site growth declined in only the two driest years (2001–2002) of the five ‘dry’ years, resulting in larger error bars for the High site in Fig. 3a.

Interannual growth and gas exchange

PDSI and growth generally decreased over the study period (Fig. 4a and b). Throughout the study period, BAI/BA of live trees was greater at higher elevations (Fig. 4b, Table 3, $P = 0.01$). Low site dead trees had higher BAI/BA than Low site live trees until the final 2 years of the study ($P < 0.01$). $p_a - p_c$ increased with decreasing site elevation ($P = 0.01$ for all years), and was slightly lower for dead than live trees at the Low site (though not significantly, $P > 0.10$, Table 3, Fig. 4c). Δ exhibited similar patterns to $p_a - p_c$ (Table 3). Notably, the range of $p_a - p_c$ values was smallest for trees that died, and increased with elevation for live trees (Table 3).

Climate sensitivity

Climate variables generally correlated well with $p_a - p_c$ and growth except in the case of trees that died, which showed no $p_a - p_c$ correlation with climate (Table 2). $p_a - p_c$ showed increasing climate dependency with increasing elevation, as indicated by the coefficients of determination. PDSI and VPD generally had the strongest fit statistics across all elevations. Δ exhibited similar coefficients with climate as $p_a - p_c$ (data not shown).

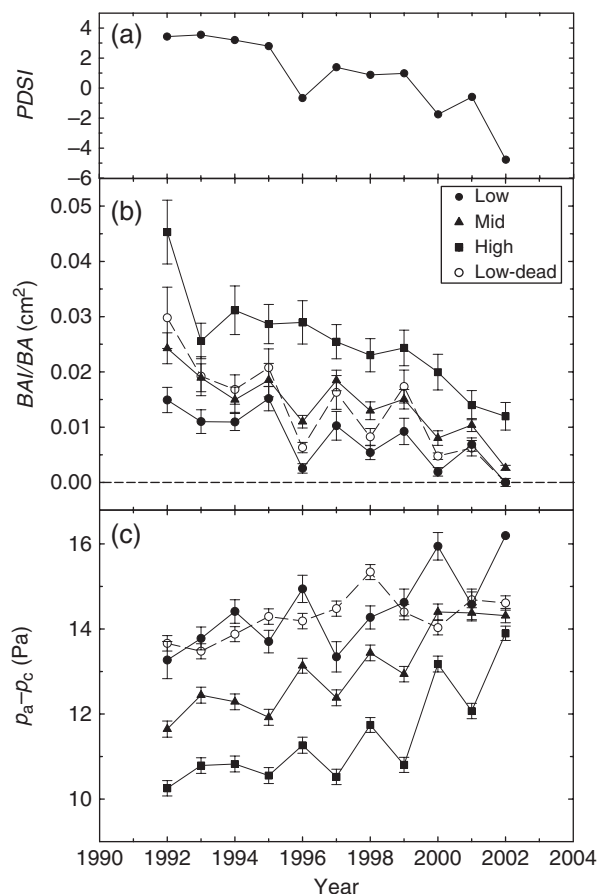


Fig. 4 (a) Mean annual PDSI for northern New Mexico for 1992–2002. Positive values of PDSI are wet periods and negative values are dry periods. (b) BAI/BA, and (c) $p_a - p_c$ of trees at the Low-dead, Low, Mid and High elevation sites for 1992–2002. Scale bars are SE.

Trees that died exhibited a significantly steeper slope of BAI/BA vs. PDSI, or climate sensitivity than live trees (Fig. 5a, $P < 0.01$). There was no difference in climate sensitivity for live trees ($P > 0.10$). The ratio of growth for wet vs. dry years (W:D) for BAI/BA exhibited a significant relationship with elevation for live trees (Table 3, $P < 0.01$). Dead trees had significantly greater W:D (BAI/BA) than live trees (Table 3, $P < 0.01$).

In stark contrast to growth, the climate sensitivity of $p_a - p_c$ diverged between live and dead trees (Fig. 5b). There was no significant relationship between $p_a - p_c$ and PDSI for trees that died ($P > 0.10$). There was a significant slope between $p_a - p_c$ and PDSI for trees that survived at each site ($P < 0.01$ for all three elevations). These slopes were similar for all three elevations ($P > 0.10$). Similar results were observed for Δ (data not shown). The W:D analyses were consistent with the slope tests, with limited sensitivity of $p_a - p_c$

Table 3 Stand level mean values of BAI (cm² yr⁻¹), BAI/BA (cm² cm⁻² yr⁻¹), Δ (‰), $p_a - p_c$ (Pa), the ratio of each of these for five wet vs. five dry years (W:D), leaf nitrogen per unit dry weight (%) and per unit leaf area (g cm⁻²), specific leaf area (cm² g⁻¹), tree height (m), height/BA (m/m²), modeled g_s , and the range for g_s and $p_a - p_c$

Site	Low-dead	Low-live	Mid	High
Mean BAI	11.76 (2.54)	13.93 (2.63)	17.34 (1.86)	32.56 (2.48)
Mean BAI/BA $\times 10^3$	12.8 (2.9)	8.02 (1.54)	13.8 (1.7)	25.3 (2.5)
Mean Δ	15.98 (0.10)	16.23 (0.19)	16.56 (0.19)	17.28 (0.26)
Mean $p_a - p_c$	14.29 (0.13)	14.46 (0.30)	13.03 (0.30)	11.44 (0.35)
W:D (BAI)	4.64 (0.31)	2.75 (0.18)	1.77 (0.18)	1.35 (0.13)
W:D (BAI/BA)	4.99 (0.35)	2.93 (0.19)	1.96 (0.18)	1.55 (0.14)
W:D (Δ)	1.01 (0.01)	1.03 (0.05)	1.07 (0.06)	1.08 (0.07)
W:D ($p_a - p_c$)	0.96 (0.02)	0.92 (0.04)	0.88 (0.04)	0.86 (0.05)
Leaf N	na	1.28 (0.10)	1.33 (0.03)	1.41 (0.03)
Leaf N	na	0.055 (0.001)	0.056 (0.001)	0.066 (0.002)
SLA	na	23.56 (0.51)	23.66 (0.71)	21.36 (1.10)
Mean height	14.42 (0.81)	14.79 (1.39)	21.67 (0.69)	21.84 (0.97)
Height/BA	156.93 (1.23)	78.47 (2.21)	172.46 (1.02)	169.73 (1.32)
Minimum modeled g_s	0.08	0.12	0.14	0.23
Maximum modeled g_s	0.31	0.47	0.52	0.88
Range modeled g_s	0.23	0.35	0.38	0.65
Range $p_a - p_c$	1.86	2.68	2.76	3.64

Dead trees lacked needles and could not be sampled for leaf characteristics. Modeled g_s is calculated on a relative scale (see 'Materials and methods'). Values in parentheses are SE.

($P = 0.11$) and Δ ($P = 0.19$) to PDSI for trees that died (W:D values near 1.0), whereas trees that survived at each site exhibited W:D values of $p_a - p_c$ and Δ significantly different than 1.0 ($P < 0.01$, Table 3).

Dependence of growth on gas exchange

All trees exhibited significant slopes of the relationship between growth and $p_a - p_c$ ($P < 0.01$ for all live trees, $P = 0.03$ for dead trees, Fig. 6). This slope was similar for trees that survived at all three elevations regardless of whether BAI or BAI/BA was utilized as the measure of growth ($P < 0.01$). In contrast, the slope of this relationship was significantly steeper for trees that died at the Low site ($P = < 0.01$, Fig. 6).

Leaf characteristics

SLA must decrease and leaf N must increase with decreasing elevation for either of these variables to confound the interpretation of $p_a - p_c$ as an index of g_s . SLA was not different between the Low and Mid sites, but was lower at the High site ($P = 0.02$, Table 3). This indicates that g_m may have been lower at the High site than the other two sites. Leaf N per gram dry matter and per unit leaf area increased with elevation (Table 3), indicating that photosynthetic capacity may have increased with increasing elevation. Thus, neither g_m nor photosynthetic capacity appears to be the cause of the

observed shifts in $p_a - p_c$. Instead, these patterns suggest the isotopic shifts with elevation are an even stronger metric of g_s because they would force $p_a - p_c$ in the opposite elevation trend than observed.

Hydraulic modeling

Predictions of relative gas exchange via Eqn (2) using only site specific, growing season VPD and precipitation (as an index of Ψ_s) suggested that g_s declined with elevation (Fig. 7). Notably, when Ψ_s is consistently positive and VPD consistently low (e.g. high elevation) g_s is more sensitive to VPD, i.e. it has a steeper slope than trees located at lower, drier elevations (Fig. 7). The minimum, maximum, and most importantly, the range of modeled g_s was lowest for the Low site dead trees and increased for live trees with increasing site elevation (Table 3). All sites were significantly different ($P < 0.01$), including the live versus dead trees at the Low site.

Modeled g_s strongly corroborated the empirical $p_a - p_c$ results (Fig. 8). For live trees only, the regression equation was: $p_a - p_c = 0.110g_s + 1.83$, $P < 0.001$, $r^2 = 0.76$. For trees that died during the drought, we varied the k_1 parameterization of modeled g_s [Eqn (2)] until we obtained the highest regression fit within Fig. 8 to assess the likely relative ranking of k_1 for live vs. dead trees. The highest fit of g_s to $p_a - p_c$ using all live and dead trees was found when k_1 of dead trees was set to 0.65 at the low site ($p_a - p_c = 0.113g_s + 1.85$, $P < 0.001$, $r^2 =$

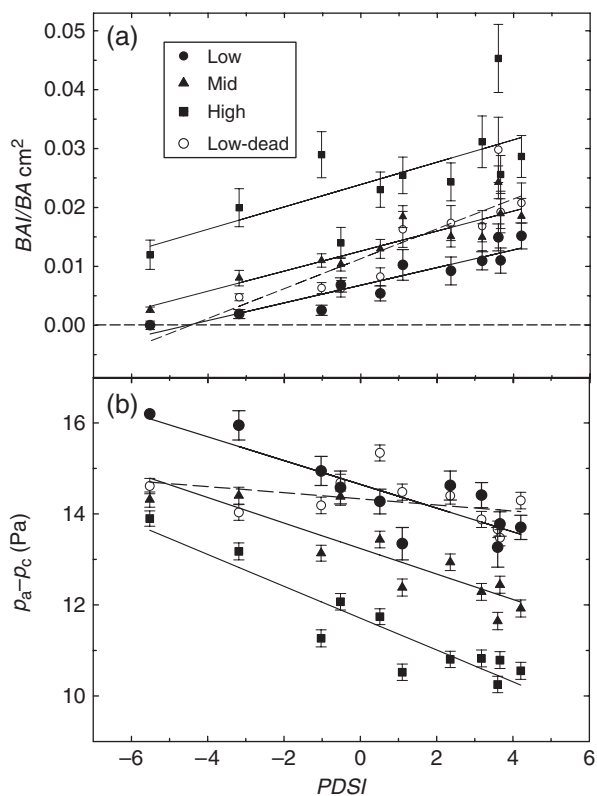


Fig. 5 (a). Mean annual BAI/BA vs. PDSI for 1992–2002. The regression lines are: BAI/BA (Low-dead) = $0.0028\text{PDSI} + 0.011$, $P < 0.01$, $r^2 = 0.85$ (dashed line), BAI/BA (Low) = $0.0015\text{PDSI} + 0.007$, $P < 0.01$, $r^2 = 0.87$, BAI/BA (Mid) = $0.0018\text{PDSI} + 0.012$, $P < 0.01$, $r^2 = 0.83$, BAI/BA (High) = $0.0020\text{PDSI} + 0.024$, $P < 0.05$, $r^2 = 0.49$. (b) Mean $p_a - p_c$ vs. growing season PDSI (March–September) for 1992–2002. The regression lines are: $p_a - p_c$ (Low) = $0.26\text{PDSI} + 14.7$, $P < 0.01$, $r^2 = 0.62$, $p_a - p_c$ (Mid) = $0.28\text{PDSI} + 13.24$, $P < 0.01$, $r^2 = 0.76$, and $p_a - p_c$ (High) = $0.35\text{PDSI} + 11.71$, $P < 0.01$, $r^2 = 0.86$. There was no significant relationship for the Low-dead site ($P = 0.23$, $r^2 = 0.16$, dashed line).

0.77). For comparison, k_1 was 1.0, 0.9 and 0.8 for the live Low, Mid and High sites, respectively.

Discussion

Building on the widespread observations of enhanced growth-sensitivity to climate in trees that die, we proposed that if carbon starvation drives mortality (McDowell *et al.*, 2008a), and if gas exchange and growth are directly linked, then gas exchange should be more steeply coupled to climate, i.e. more sensitive, in trees that die than trees that survive. We tested this idea via three linked hypotheses. Our first hypothesis was supported; mortality was associated with greater growth sensitivity to climate (Fig. 5a, Table 3), which is consistent with published observations. Our second hypoth-

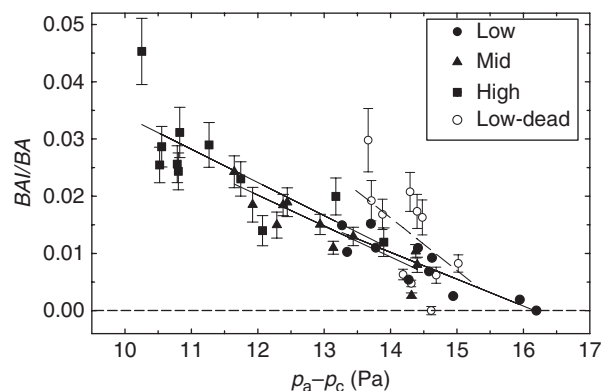


Fig. 6 Mean BAI/BA vs. $p_a - p_c$. The regression lines are BAI/BA (Low) = $0.0059p_a - p_c + 0.093$, $P < 0.01$, $r^2 = 0.87$, BAI/BA (Mid) = $0.0054p_a - p_c + 0.085$, $P < 0.01$, $r^2 = 0.82$, and BAI/BA (High) = $0.0058p_a - p_c + 0.092$, $P < 0.01$, $r^2 = 0.59$. There was no significant relationship for the Low-dead site ($P = 0.08$, $r^2 = 0.30$, dashed line).

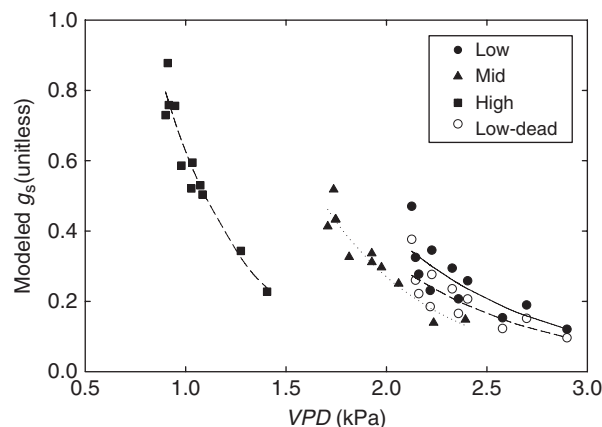


Fig. 7 Stomatal conductance modeled from Eqn (2) vs. elevation-specific VPD. The nonlinear regression lines are: g_s (Low-dead) = $4.80e^{-1.35\text{VPD}}$, $P < 0.01$, $r^2 = 0.77$, g_s (Low) = $5.99e^{-1.35\text{VPD}}$, $P < 0.01$, $r^2 = 0.77$, g_s (Mid) = $10.61e^{-1.84\text{VPD}}$, $P < 0.01$, $r^2 = 0.92$, and g_s (High) = $6.84e^{-2.40\text{VPD}}$, $P < 0.01$, $r^2 = 0.96$.

esis was refuted; mortality was not associated with greater sensitivity of $p_a - p_c$ to climate. Unlike the surviving trees, which showed a strong climatic sensitivity of gas exchange, there was no apparent response of $p_a - p_c$ to PDSI for trees that died (Fig. 5b, Table 3). Our third hypothesis, that variation in growth was correlated with $p_a - p_c$, was supported for all live and dead trees at all three elevations, with the steepest relationship for trees that died (Fig. 6). The dead trees' steep relationship between $p_a - p_c$ and growth concurrent with their insensitivity of $p_a - p_c$ to climate requires a revised interpretation of the cause of mortality. We hypothesize that carbon starvation remains a predisposing mechan-

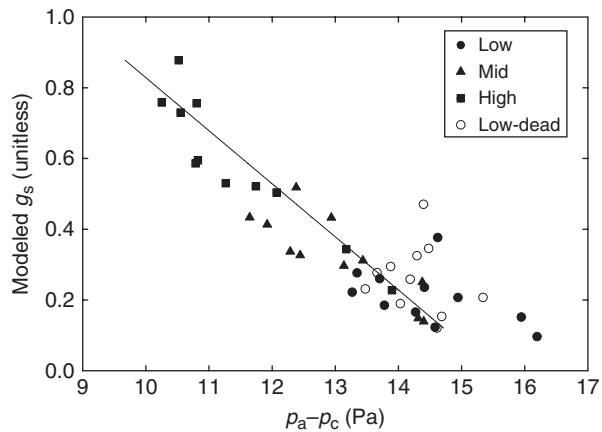


Fig. 8 $p_a - p_c$ derived from tree ring $\delta^{13}\text{C}$ data vs. modeled stomatal conductance from Eqn (2). The regression line is: $p_a - p_c$ (all sites) = $0.113g_s + 1.85$, $P < 0.001$, $r^2 = 0.77$.

ism of vulnerability to bark beetle attack, but that it occurred due in part to chronic water stress and a subsequently narrow range of gas exchange (Figs 5–7, Table 3).

Mechanisms of mortality

The narrow range of gas exchange for trees that died was superimposed on an elevation trend of lower gas exchange as elevation decreased (Fig. 7, Table 3). This elevation trend occurred despite similar ranges of VPD and precipitation across the elevation transect, i.e. mean growing season VPD and precipitation ranges at the Low site over the 11 year study was 0.77 kPa and 260 mm, respectively, which is similar to the Mid (0.70 and 300 mm) and High sites (0.51 kPa and 280 mm). The consistent aridity at low elevation appears to limit maximum g_s and thereby the range of g_s because the lower limit of g_s is finite (Table 3). This also explains the elevation trend of reduced sensitivity of g_s to climate (Fig. 7); e.g. lower maximum g_s constrains the slope of g_s to VPD (e.g. Oren *et al.*, 1999).

That trees that died had a narrower gas exchange range than neighboring trees that survived indicates edaphic or within-tree constraints upon k_1 . There were no obvious edaphic differences between live and dead trees at low elevation. Stand density and shading were similarly low for both (Fig. 2, Table 1), and there were no apparent differences in aspect, soil depth, or pathogen load. One clear within-tree difference is their size and structure – trees that died had smaller basal areas (average basal areas of 918 and 1751 cm², respectively, $P < 0.001$) but were the same height (Table 3, $P > 0.10$), and thus had greater ratios of height/BA (Table 3, $P < 0.001$). Trees with lower basal areas and a greater

height/BA ratio may have lower k_1 due to shallower or less distributed rooting distribution (Dawson, 1996; Meier & Leuschner, 2008), reduced sapwood area (Maherali & Delucia, 2001), high leaf area:sapwood area ratios relative to soil water availability (McDowell *et al.*, 2006), or less capacitance (Phillips *et al.*, 2003; Ryan *et al.*, 2006). Results of our model sensitivity analysis are consistent with this interpretation, suggesting that dead trees may have had 35% lower k_1 than live trees (Fig. 8) at the same elevation. This interpretation is logical because k_1 integrates the hydraulic bottlenecks within the tree and soil (Sperry *et al.*, 2002), and thus a constraint on maximum k_1 will produce a narrower range of g_s and limited sensitivity to climate. In contrast, trees that survive at low elevations should be those that maximize k_1 because ponderosa pine increases k_1 to cope with the greater water deficits at lower elevations (Maherali & Delucia, 2001; Maherali *et al.*, 2002). Based on these empirical and theoretical results, we hypothesize that chronic constraints upon k_1 and g_s are predisposing factors to mortality during drought.

The steep coupling of gas exchange and growth (Fig. 6) suggests that an additional factor beyond chronically low g_s is responsible for the growth-sensitivity of trees that died (Figs 5a and 6). Potential reasons include (1) dynamic changes in canopy leaf area, (2) water stress constraints on symplastic metabolism, (3) reduced carbohydrate storage capacity, and (4) hydraulic failure. (1) Leaf shedding occurs in response to drought (Tyree *et al.*, 1993; Suarez *et al.*, 2004; Hultine *et al.*, 2006), which reduces whole-tree photosynthesis and stemwood growth with minimal changes in Δ (McDowell *et al.*, 2006). This would allow large changes to occur in BAI/BA without concomitant changes in tree ring $\delta^{13}\text{C}$, consistent with observations of *Fagus sylvatica* (Peñuelas *et al.*, 2008). (2) Water stress constraints on symplastic carbon metabolism could occur if cell expansion, division, and carbohydrate use are limited by water potential (Körner, 2003; Alves & Setter, 2004; Woodruff *et al.*, 2004; Ryan *et al.*, 2006). In severe drought conditions, trees with less favorable water status could cease both growth and resin production, leading to a steep relationship between BAI/BA and g_s , and elevated vulnerability to pathogen attack. (3) Reduced carbohydrate storage capacity has not been investigated in trees that die; however, if their cellular or whole-tissue storage capacity is low, then the length of time a tree can survive without positive net photosynthesis will be diminished and carbon starvation, or cessation of resin production, will ensue sooner (McDowell *et al.*, 2008a). Lastly, (4) hydraulic failure may have occurred if g_s failed to regulate transpiration above its cavitation threshold (Sperry *et al.*, 2002; McDowell *et al.*, 2008a). This is consistent with a lack of g_s sensitivity to climate

and has been empirically shown in seedlings (Brodrribb & Cochard, 2009) and shrubs (Davis *et al.*, 2002), but not in mature trees (Cinnirella *et al.*, 2002). Other factors that may exacerbate, or be exacerbated by, chronic water stress include transient reductions in g_m (Flexas *et al.*, 2004; Warren *et al.*, 2004) photosynthetic capacity (Martin & Ruiz-Torres, 1992; Escalona *et al.*, 1999; Parry *et al.*, 2002) hydraulic conductance (Maherali *et al.*, 2002; Meier & Leuschner, 2008) and regional population dynamics of insects (Raffa *et al.*, 2008). Insect presence was ubiquitous at our low elevation site in 2002–2003, so the population dynamics at the regional level *per se* cannot explain why some trees died and some survived at the low elevation site.

A note on elevation studies of tree ring $\delta^{13}C$

It appears that elevation- $\delta^{13}C$ studies fall into two groups: (1) those that sampled plants with access to perennial water sources, and thus factors such as photosynthetic capacity and g_m dominated p_a p_c (Vitousek *et al.*, 1990; Körner *et al.*, 1991; Marshall & Zhang, 1994; Sparks & Ehleringer, 1997; Cordell *et al.*, 1999; Hultine & Marshall, 2000; Kogami *et al.*, 2001; Li *et al.*, 2004) and (2) those that sampled plants without access to perennial water sources, in which case g_s dominated p_a p_c (Treydte *et al.*, 2001; Van de Water *et al.*, 2002; Adams & Kolb, 2004; Peñuelas *et al.*, 2008, this study). This is consistent with the observation that conifer stemwood $\delta^{13}C$ increases with decreasing elevation in semi-arid areas, but not in relatively mesic areas (Warren *et al.*, 2001). Future research using $\delta^{13}C$ of organic matter along elevation gradients should take in to account the confounding effects of pressure and moisture within their experimental design (Körner, 2007). Particular to retrospective studies of mortality such as ours, it will be important to either avoid, or account for, confounding of water availability.

Conclusions and climate change implications

Ecotonal ponderosa pine trees that died during drought had the greatest climatic sensitivity of growth (BAI/BA), the least climatic sensitivity of gas exchange (p_a p_c and modeled g_s), and the steepest coupling between growth and gas exchange relative to trees that survived. In comparison, all live trees conformed to similar climatic sensitivities and dependency of growth and gas exchange. It appears that chronic hydraulic constraints on g_s result in an insufficient buffer between wet and dry periods, leaving only a narrow margin between ponderosa pine survival and death at dry ecotones. This result is consistent with carbon starvation as a mechanism of death, but does not eliminate nor identify the

contribution of other mechanisms that are directly or indirectly driven by hydraulic constraints (McDowall *et al.*, 2008a).

Global climate change projections show increasing mean and extreme temperatures, along with consistent projections of increasing drought severity and frequency in many parts of the world, particularly in mid-latitude regions (Lawford *et al.*, 1993; Hanson & Weltzin, 2000; Rosenberg *et al.*, 2003; Weltzin *et al.*, 2003; Cook *et al.*, 2004; McCabe *et al.*, 2004; IPCC, 2007; Seager *et al.*, 2007). Impacts of drought appear to outweigh the benefits of CO₂ fertilization on tree growth and survival, particularly in the drier portions of species distributions (Martínez-Vilalta *et al.*, 2008; Peñuelas *et al.*, 2008, this study). It appears likely that a hydraulic mechanism underlies hydraulic failure, carbon starvation, or symplastic limitations, thus we can expect continued forest mortality in dry, temperate regions if climate projections of increased water stress are accurate. Greater understanding of the coupled hydraulic-carbon mechanisms of tree mortality is needed to improve our ability to forecast climate-induced forest mortality.

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