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 (pa–pc) derived from tree ring carbon isotope ratios (δ13C), corrected for temporal trends in atmospheric CO2 and δ13C and elevation trends in pressure. Trees that survived the drought exhibited strong correlations among and between BAI, BAI/BA, pa–pc, and climate. In contrast, trees that died exhibited greater growth sensitivity to climate than trees that survived, no sensitivity of pa–pc to climate, and a steep relationship between pa–pc and BAI/BA. The pa–pc 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 CO$_2$ 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; Hansson & 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 verses 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 xerophytic 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):

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

(1)

In this representation of Fick’s law, $c_a$ and $c_c$ are atmospheric and chloroplast CO$_2$ 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 ($\delta^{13}$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 $\delta^{13}$C of plant material has frequently been used as an index of gas exchange because it is dependent on the balance of CO$_2$ 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 $\delta^{13}$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 $\delta^{13}$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
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):

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

in which $k_i$ is whole plant hydraulic conductance, $\Psi_s$ is soil water potential (MPa), $\Psi_l$ is daytime leaf water potential, and $VPD$ is vapor pressure deficit (VPD, kPa). Manipulating $VPD$ and $\Psi_s$ 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 $\Psi_s$ 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, and (3) mortality was related to $\delta^{13}C$. Additional hypotheses regarding mortality due to drought stress were also tested

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).
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 δ^13C, 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 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

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.

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 (m^2 ha^-1), and mean annual climate for the study period (1992–2002) including precipitation (mm), maximum and minimum temperature (°C) and vapor pressure deficit (kPa) during daylight hours

<table>
<thead>
<tr>
<th>Site</th>
<th>Low</th>
<th>Mid</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coordinates</td>
<td>35° 19' N, 106° 27' W</td>
<td>35° 19' N, 106° 40' W</td>
<td>35° 19' N, 106° 36' W</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>2000</td>
<td>2310</td>
<td>2750</td>
</tr>
<tr>
<td>Density (# ha^-1)</td>
<td>165 (19)</td>
<td>587 (62)</td>
<td>430 (57)</td>
</tr>
<tr>
<td>Basal area (m^2 ha^-1)</td>
<td>8.8 (1.3)</td>
<td>32.1 (2.2)</td>
<td>29.2 (3.1)</td>
</tr>
<tr>
<td>Annual Precipitation (mm)</td>
<td>350 (23)</td>
<td>440 (30)</td>
<td>500 (31)</td>
</tr>
<tr>
<td>Maximum Temperature (°C)</td>
<td>18.2 (0.2)</td>
<td>15.7 (0.2)</td>
<td>9.5 (0.2)</td>
</tr>
<tr>
<td>Minimum Temperature (°C)</td>
<td>1.2 (0.1)</td>
<td>2.3 (0.2)</td>
<td>0.0 (0.25)</td>
</tr>
<tr>
<td>VPD (kPa)</td>
<td>1.6 (0.03)</td>
<td>1.3 (0.03)</td>
<td>0.75 (0.02)</td>
</tr>
</tbody>
</table>

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 at sites 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, cm$^2$ 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. 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, cm$^2$ cm$^{-2}$ 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 $^{13}$CO$_2$ relative to $^{12}$CO$_2$ because $^{13}$CO$_2$ 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 ($\Delta$) results in $\delta^{13}C$ 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):

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

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 $c_a$ is often written as internal CO$_2$ or $c_i$ but we are using $c_c$ to be consistent with Eqn (1)]. While $\Delta$ 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 $\Delta$ 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 $\mu$m, respectively, Orvis & Grissino-Mayer, 2002). When necessary we also used FEPA 400 grit sandpaper (33.5–36.5 $\mu$m, 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 $\delta^{13}C$ 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 $\delta^{13}C$ because numerous studies have reported constant relationships between cellulose and whole-wood $\delta^{13}C$ 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 $\delta^{13}C$ was 0.05% (n = 52).
Table 2  Coefficients of determination ($r^2$) for regressions between climate, $p_a$ $p_c$ and BAI

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Low-dead</th>
<th>Low-live</th>
<th>Mid</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p_a$</td>
<td>$p_c$</td>
<td>BAI/BA</td>
<td>$p_a$</td>
<td>$p_c$</td>
</tr>
<tr>
<td>Min $R_h$</td>
<td>0.00</td>
<td>0.85</td>
<td>0.51</td>
<td>0.59</td>
</tr>
<tr>
<td>VPD</td>
<td>0.01</td>
<td>0.84</td>
<td>0.63</td>
<td>0.75</td>
</tr>
<tr>
<td>Precipitation</td>
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<td>0.01</td>
<td>0.13</td>
</tr>
<tr>
<td>Min $T_a$</td>
<td>0.09</td>
<td>0.31</td>
<td>0.27</td>
<td>0.34</td>
</tr>
<tr>
<td>Max $T_a$</td>
<td>0.01</td>
<td>0.76</td>
<td>0.56</td>
<td>0.74</td>
</tr>
<tr>
<td>PDSI</td>
<td>0.00</td>
<td>0.86</td>
<td>0.48</td>
<td>0.87</td>
</tr>
<tr>
<td>Average</td>
<td>0.02</td>
<td>0.67</td>
<td>0.41</td>
<td>0.57</td>
</tr>
</tbody>
</table>

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 $z = 0.05$ are bolded.

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

$$\Lambda = \frac{\delta^{13}C_a - \delta^{13}C}{1 + \delta^{13}C}.$$  \hspace{1cm} (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; Keelings 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 $\Lambda$ and $p_a$ $p_c$ for both between and within site analyses. The results of regressions of both $\Lambda$ 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 $\Lambda$ vs. climate variables (those shown in Table 2) the following ways: (1) re-arrangement of $\Lambda$ values for neighboring rings (e.g., swapping 1998 $\Lambda$ with 1999 $\Lambda$) – this represents the most likely way contamination could occur; (2) using only $\Lambda$ 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 $\Lambda$ results confirms that even if carbon contaminated across rings, there is no ring that has $\Lambda$ values sufficiently negative to provide a significant regression of $\Lambda$ 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 $g_c$. 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., 1991), 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 $^\delta$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, $A$, 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 $A$, $p_a$ $p_c$, 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, $A$ 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 $A$ 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 ($T_a$, °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, $\Psi_s$ and $k_l$ 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 $\Psi_s$ 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 $\Psi_s$ $\Psi_l$ ranging between 0.35 (lowest precipitation) and 1.0 (highest precipitation) for each site. We assumed that $\Psi_l$ is constant (isohydric) regardless of site water availability (Maherali & Delucia, 2001) and that $k_l$ 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 $k_l$ 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 $k_l$ constant over time. To examine the role of $k_l$ in tree mortality, we varied $k_l$ 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 $k_l$ in dead trees and because $k_l$ 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: \(\text{mean BAI wet} – \text{mean BAI dry}/\text{maximum BAI}\), 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, \(P > 0.1\), Table 3, Fig. 4c). \(\Delta\) exhibited similar patterns to \(p_a-p_c\) (Table 3). Notably, the range of \(p_a\) to \(p_c\) 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. \(\Delta\) exhibited similar coefficients with climate as \(p_a\) \(p_c\) (data not shown).

![Fig. 4](image-url) (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 \((P > 0.1)\). 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 \((P > 0.1)\). 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 \((P > 0.1)\). Similar results were observed for \(\Delta\) (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 (cm$^2$ yr$^{-1}$), BAI/BA (cm$^2$ cm$^{-2}$ yr$^{-1}$), $\Delta$ (%), $p_a$ (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 (cm$^2$ g$^{-1}$), tree height (m), height/BA (m/m$^2$), modeled $g_s$ and the range for $g_s$ and $p_a$, $p_c$.

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

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 $\Delta$ ($P = 0.19$) 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 $\Delta$ 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 $g_{sm}$ 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 $g_{sm}$ 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 $\Psi_s$) suggested that $g_s$ declined with elevation (Fig. 7). Notably, when $\Psi_s$ 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 verses 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 $k_l$ parameterization of modeled $g_s$ [Eqn (2)] until we obtained the highest regression fit within Fig. 8 to assess the likely relative ranking of $k_l$ 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 $k_l$ of dead trees was set to 0.65 at the low site ($p_a$, $p_c = 0.113g_s + 1.85$, $P < 0.001$, $r^2 =$ 0.76).

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 hypothesis 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 mechanism for widespread tree mortality, and that the severity and rapidity of this effect may be linked to climatic conditions during the growing season.
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 \( k_t \). 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 cm\(^2\), 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 \( k_t \) 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 \( k_t \) than live trees (Fig. 8) at the same elevation. This interpretation is logical because \( k_t \) integrates the hydraulic bottlenecks within the tree and soil (Sperry et al., 2002), and thus a constraint on maximum \( k_t \) 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 \( k_t \) because ponderosa pine increases \( k_t \) 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 \( k_t \) 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 (Tyyre et al., 1993; Suarez et al., 2004; Hultine et al., 2006), which reduces whole-tree photosynthesis and stemwood growth with minimal changes in \( \Delta \) (McDowell et al., 2006). This would allow large changes to occur in BAI/BA without concomitant changes in tree ring \( \delta^{13}C \), 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 (Brodribb & 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 into 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 (McDowell 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 CO$_2$ 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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