

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

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5 **Running title:** Chronic water stress drives mortality at a ponderosa pine ecotone
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1 **Abstract:** Drought- and insect-associated tree mortality at low-elevation ecotones is a
2 widespread phenomenon but the underlying mechanisms are uncertain. Enhanced growth
3 sensitivity to climate is widely observed among trees that die, indicating that a predisposing
4 physiological mechanism(s) underlies tree mortality. We tested three, linked hypotheses
5 regarding mortality using a ponderosa pine (*Pinus ponderosa*) elevation transect that experienced
6 low-elevation mortality following prolonged drought. The hypotheses were: 1) mortality was
7 associated with greater growth sensitivity to climate, 2) mortality was associated with greater
8 sensitivity of gas exchange to climate, and 3) growth and gas exchange were correlated. Support
9 for all three hypotheses would indicate that mortality results at least in part from gas exchange
10 constraints. We assessed growth using basal area increment normalized by tree basal area
11 (*BAI/BA*) to account for differences in tree size. Whole-crown gas exchange was indexed via
12 estimates of the CO₂ partial pressure difference between leaf and atmosphere (p_a-p_c) derived
13 from tree ring carbon isotope ratios ($\delta^{13}\text{C}$), corrected for temporal trends in atmospheric CO₂ and
14 $\delta^{13}\text{C}$ and elevation trends in pressure. Trees that survived the drought exhibited strong
15 correlations among and between *BAI*, *BAI/BA*, p_a-p_c , and climate. In contrast, trees that died
16 exhibited greater growth sensitivity to climate than trees that survived, no sensitivity of p_a-p_c to
17 climate, and a steep relationship between p_a-p_c and *BAI/BA*. The p_a-p_c results are consistent with
18 predictions from a theoretical hydraulic model, suggesting trees that died had a limited buffer
19 between mean water availability during their lifespan and water availability during drought - i.e.,
20 chronic water stress. It appears that chronic water stress predisposed low-elevation trees to
21 mortality during drought via constrained gas exchange. Continued intensification of drought in
22 mid-latitude regions may drive increased mortality and ecotone shifts in temperate forests and
23 woodlands.

1 **Introduction** Drought-induced vegetation mortality has rapid, widespread and long-lasting
2 impacts on the biotic composition of landscapes (Allen and Breshears 1998, Berg et al. 2006).
3 Mortality-driven changes in ecosystem structure and function can result in ecotone shifts (Allen
4 and Breshears 1998), altered wildfire hazard and increased erosion (Allen 2007), decreased
5 carbon storage (Breshears and Allen 2002, Kurz et al. 2008), and shifts in surface hydrology
6 (Newman et al. 2006). Recent drought-related forest mortality has been observed throughout the
7 world (e.g. Condit et al. 1995, Swetnam and Betancourt 1998, Fensham and Holman 1999,
8 Gonzalez 2001, Suarez et al. 2004, Bigler et al. 2006, van Mentegm and Stephenson 2007,
9 McDowell et al. 2008a, Raffa et al. 2008, Fensham et al. 2009, Allen et al. in review) and may be
10 associated with increased surface temperatures (Breshears et al. 2005, van Mentegm et al. 2009).
11 This mortality is occurring despite the sometimes observed CO₂ fertilization of tree growth
12 (Tang et al. 1999, Martínez-Vilalta et al. 2008) and water use efficiency (Saurer et al. 2004,
13 Peñuelas et al. 2008). Climate-associated mortality is exemplified in western North America,
14 where widespread mortality of dominant species, such as most members of the *Pinaceae*, has
15 recently been observed throughout the length of the Rocky Mountains (Raffa et al. 2008).
16 Climate-induced vegetation mortality is a growing global concern (Allen and Breshears 2007)
17 due to the projections of increasing drought severity and frequency in many regions of the world
18 (Lawford et al. 1993, Hanson and Weltzin 2000, Rosenberg et al. 2003, Weltzin et al. 2003,
19 Cook et al. 2004, McCabe et al. 2004, IPCC 2007, Seager et al. 2007).

20 There is currently no consistent mechanism identified to explain why trees die during
21 drought and associated pathogen outbreaks (e.g. bark beetle, *Ips* Raffa et al. 2008, Bentz et al. *in*
22 *press*), but the general consensus is that mortality depends in part on the whole tree carbon
23 budget (e.g. Manion 1981, Waring 1987, McDowell et al. 2008a). This is reflected in empirical

1 observations that consistently show greater sensitivity of stemwood growth to climate in trees
2 that die compared to those that survive (Pedersen 1998, Demchik and Sharpe 2000, Ogle et al.
3 2000, Suarez et al. 2004). Greater growth sensitivity to climate, i.e. steeper slopes of a
4 regression of growth verses climate, has also been seen in trees from low elevation ecotones in
5 comparison to higher elevation locations (Adams and Kolb 2004, Peñuelas et al. 2008), and
6 lower elevation ecotones typically experience greater mortality (Allen and Breshears 1998).
7 This common observation may be explained by the logical cascade of events in trees that die,
8 from water stress to particularly reduced photosynthesis and subsequently reduced growth and
9 production of resin to fend off insect attack (Gaylord et al. 2007).

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

$$16 \quad A \approx g \cdot (c_a - c_c) \quad (1).$$

17 In this representation of Fick's law, c_a and c_c are atmospheric and chloroplast CO_2 concentrations
18 and g represents stomatal (g_s) and mesophyll conductance (g_m). It is well established that g_s is
19 curtailed during dry periods to minimize hydraulic failure (Sperry et al. 2002), and therefore
20 periods of extreme drought can conceivably result in little or no photosynthesis (Gaylord et al.
21 2007, McDowell et al. 2008a). Extended periods without photosynthesis may cause mortality
22 because, while carbon allocation to wood growth may cease temporarily without death, carbon
23 allocation to maintenance respiration (Ryan et al. 1995, Amthor 2000) must continue at some

1 basal level or mortality is inevitable (Marshall and Waring 1985). Likewise, defense against
2 insect attack requires sufficient carbon reserves to generate defensive compounds and sufficient
3 phloem pressure to occlude insect entry holes (Coley et al. 1985, Cobb et al. 1997, Wallin et al.
4 2003, McDowell et al. 2007). Therefore, to the extent that wood growth is correlated with
5 photosynthesis (e.g. Waring et al. 1998, Litton et al. 2007) and with resin flow (McDowell et al.
6 2007), it is logical to expect that wood growth is an indicator of tree predisposition to mortality.
7 This hypothesis is consistent with theoretical, empirical, and model-based mortality research
8 (reviewed in McDowell et al. 2008a).

9 Two tools that have proven useful for investigations of climate constraints on growth are
10 1) elevation transects as a study design, and 2) stable carbon isotope ratios ($\delta^{13}\text{C}$) as an index of
11 gas exchange. Elevation transects allow understanding of growth constraints associated with
12 climate (e.g. Lajtha and Getz 1993, Adams and Kolb 2004) and ecotone dynamics (Gitlin et al.
13 2006, Beckage et al. 2008, Kelly and Goulden 2008) because temperatures are generally cooler
14 and moisture availability greater with increasing elevation (Körner 2007) and because lower
15 elevation ecotones are typically dynamic in response to moisture stress (Allen and Breshears
16 1998). The $\delta^{13}\text{C}$ of plant material has frequently been used as an index of gas exchange because
17 it is dependent on the balance of CO_2 diffusion into and out of the chloroplast, which results
18 from photosynthesis and g (equation 1, see methods for further description, Seibt et al. 2008).
19 Tree-ring $\delta^{13}\text{C}$ is particularly useful because it provides a whole-crown, assimilation weighted
20 record of gas exchange that can be discretized to individual years, allowing analyses of the
21 response of individual trees to climatic variation (Francey and Farquhar 1982, Walcroft et al.
22 1997, Pate 2001). There is a long tradition of combining $\delta^{13}\text{C}$ analyses with elevation transects
23 (e.g. Vitousek et al. 1990, Körner et al. 1991, Marshall and Zhang 1994, Sparks and Ehleringer

1 1997, Cordell et al. 1999, Hultine and Marshall 2000, Warren et al. 2001, Van de Water et al.
2 2002, Adams and Kolb 2004, Peñuelas et al. 2008), though no prior studies have used these tools
3 to investigate mechanisms of mortality.

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

$$8 \quad g_s = \frac{k_l(\Psi_s - \Psi_l)}{VPD} \quad (2),$$

9 in which k_l is whole plant hydraulic conductance, Ψ_s is soil water potential (MPa), Ψ_l is daytime
10 leaf water potential, and VPD is vapor pressure deficit (kPa). Manipulating VPD and Ψ_s in
11 equation (2) allows one to predict the response of g_s (and A) to drought. More complex versions
12 of this model exist (e.g. Whitehead 1998, Oren et al. 1999, Phillips et al. 2002), and more
13 complex hydraulic models exist (e.g. Williams et al. 2001, Sperry et al. 2002); however, the
14 simple framework in equation (2) allows interpretation of gross level impacts of chronic
15 differences in Ψ_s and VPD on whole-tree gas exchange in the absence of detailed
16 parameterization data (McDowell et al. 2005, 2008b).

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

1 We tested three hypotheses: 1) mortality was associated with greater growth sensitivity to
2 climate, 2) mortality was associated with greater sensitivity of gas exchange to climate, and 3)
3 variation in growth was correlated with gas exchange. Hypotheses (1) and (3) were tested
4 empirically using tree ring growth and $\delta^{13}\text{C}$, and hypothesis (2) was tested both empirically and
5 theoretically with the Whitehead model, in which the model was employed to assess gas
6 exchange patterns in trees that survived and died. Confirmation of these three hypotheses would
7 support the idea that the mechanism of mortality was related to gas exchange constraints on
8 photosynthesis.

9
10 **Methods. Study sites** Ponderosa pine is a widespread conifer in North America, occurring from
11 central Mexico to southern Canada (Waring and Law 2001) and is an economically important
12 species in both public and private forests. This species is expected to undergo widespread
13 mortality in the 21st century in response to climate change (Coops et al. 2005). Our study was
14 conducted in three stands of ponderosa pine situated along a 750 m elevation transect across 15
15 km within Bandelier National Monument (Figure 1), located in the Jemez Mountains of northern
16 New Mexico (Table 1). The soil parent materials at all three sites are volcanic in origin, ranging
17 from rhyolite to tuff with some pumice components. Soils are Alfisols on level to gentle terrain
18 at all three sites, with more pumice-linked Mollisol elements at mid and low elevation sites
19 (NRCS 2007). Dominant vegetation varies along the elevation gradient. The low-elevation site
20 contains multiple age classes (up to 300 years) of ponderosa pine in an open stand mixed with an
21 understory of piñon (*Pinus edulis*) and juniper (*Juniperus monosperma*, Figure 2). The mid-
22 elevation site is a denser, ~close-canopied stand of largely even-aged (ca. 95 years) ponderosa
23 pine. The high-elevation site contains multi-aged (up to ~180 years) ponderosa pine mixed with

1 Douglas-fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*). Far less mortality
2 occurred at the middle or high elevation sites. At all sites, the sampled trees were canopy
3 dominants with minimal crown shading from neighboring trees. More site details can be found
4 in Table (1). For the remainder of the paper we refer to the three sites as Low, Mid, and High,
5 respectively.

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

10

11 ***Experimental Design and Statistics*** This study was originally designed in 1991 to provide
12 information on elevation patterns of growth in relation to climate, with dendrometer bands
13 placed on ten target trees at each of three distinct elevation sites. Trees were originally selected
14 to capture both dominant and co-dominant canopy classes at each site. The Low site was
15 established at the lowest-elevation fringe of ponderosa pine in this landscape in 1991. There was
16 100% mortality of the dendrometer banded trees at the Low site in 2002-2003 (Figure 1, 2),
17 whereas all Mid and High site trees survived. Although this outcome was not predictable *a*
18 *priori*, it confounds elevation and mortality for this study. We took advantage of this added
19 complexity by sampling an equal number of Low site trees that survived the drought along with
20 the original dendrobanded trees that died. We selected the nearest possible live trees to the
21 sampled dead trees, which were typically within 100m distance. This sampling design allows a
22 direct test of our hypotheses between trees that survived and died at the Low site, as well as

1 comparison of trees that died and survived at the Low site to trees that survived at higher
2 elevations.

3 To test the hypothesis that mortality was associated with greater growth sensitivity to
4 climate, we compared slopes of growth versus climate parameters via analyses of covariance,
5 and analysis of variance to compare inter-annual variability in growth within and between sites.
6 We also calculated the ratio of growth for wet versus dry years (W:D, Adams and Kolb 2004)
7 and used analyses of variance to test for W:D differences within and between sites. Palmer
8 Drought Severity Index (*PDSI*) was used as an index for characterization of wet and dry years.
9 *PDSI* is a measure of meteorological drought calculated from precipitation, temperature and
10 potential evapotranspiration, with more negative values indicative of drought (Palmer 1965).
11 The five wettest years, based on *PDSI*, were 1992-1995 and 1999, and driest years were 1996,
12 1998, and 2000-2002. We used linear regression to test the hypothesis that variation in growth
13 was associated with $\delta^{13}\text{C}$ -based estimates of Δ and p_a-p_c (described under the Methods section on
14 carbon isotopes). Analysis of variance was used for all other analyses of differences between
15 elevations such as for leaf nitrogen and specific leaf area. For the purpose of avoiding
16 confounding and making more complex our hypothesis tests, we did not assess autocorrelation
17 because it varies with elevation and is typically nonexistent for low elevation trees in
18 southwestern USA (C. Baisan, *personal communication*). All statistical analyses were conducted
19 with Systat 11.0 (Systat, 2004).

20

21 **Growth** Dendrometer bands were established on thirty ponderosa pine trees, 10 per site, in June
22 1991, with manual recording of circumference changes (0.1 mm resolution) on approximately a
23 weekly schedule during April-October, and bi-monthly during the winter. Basal area increment

1 (BAI , $\text{cm}^2 \text{yr}^{-1}$) was calculated from weekly stem circumference measurements made from 1992
2 (the first full year of growth data) through autumn 2002 (when tree mortality occurred at the Low
3 site). Ring widths were converted to BAI from 1992 to 2002 using tree-specific circumferential
4 growth (inside bark) and assuming concentric circularity. There were a different number of
5 measurements each year, precluding inter-annual analyses by day of year. Thus for inter-annual
6 comparison of temporal dynamics of responses to drought we calculated site/week means and
7 normalized them to 365 days, i.e. $\text{day } X/365$.

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

18
19 ***Carbon isotope composition*** Photosynthesis by ponderosa pine discriminates against $^{13}\text{CO}_2$
20 relative to $^{12}\text{CO}_2$ because $^{13}\text{CO}_2$ has a lower diffusivity through the stomatal pore and lower
21 reactivity with the photosynthetic enzyme ribulose 1,5 biphosphate carboxylase-oxygenase.
22 This discrimination (Δ) results in $\delta^{13}\text{C}$ of the carbon within ponderosa pine tree rings to be

1 approximately 15-25‰ below that of atmospheric CO₂. Discrimination can be expressed
2 relative to c_c/c_a (Farquhar et al. 1989):

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

4 where a is the fractionation associated with diffusion in air (4.4‰), b is the net fractionation
5 associated with carboxylation by Rubisco (27-29‰), and c_a and c_c are as described for equation
6 (1) [note that c_c is often written as internal CO₂ or c_i but we are using c_c to be consistent with
7 equation (1)]. While Δ is a useful parameter, in elevation studies it is confounded with
8 atmospheric pressure and therefore a final correction for shifts in the partial pressure of CO₂
9 must be made, which converts concentrations (c_a and c_c) to partial pressures (p_a and p_c , Hultine
10 and Marshall 2000). Gas exchange parameters such as intrinsic water use efficiency (A/g ,
11 Ehleringer 1993) can be assessed using Δ estimates and equations (1) and (3).

12 In March 2004 we collected 12mm diameter increment cores from five of the
13 dendrometer banded trees at each plot. We additionally sampled cores from five live trees at the
14 Low site in July 2007 to allow the within-site comparison of dead and live trees. Cores were
15 removed from each tree at 1.3m height. Cores were subsequently air dried for two to three
16 months prior to further analysis. We sanded the cores using successively finer sandpaper of
17 FEPA (Fed. of European Producers of Abrasives) 100, 220, and 320 grit (162, 68, and 44.7-47.7
18 μm respectively, Orvis and Grissino-Mayer 2002). When necessary we also used FEPA 400 grit
19 sandpaper (33.5-36.5 μm , Orvis and Grissino-Mayer 2002). Cores were cross dated visually
20 using narrow marker years from tree-ring chronologies collected at local sites for ponderosa pine
21 (Chris Baisan *personal communication*). In all instances the outer ring date was known, being
22 the collection year for the living trees sampled and from monitoring of the mortality at the Low
23 site. Each ring was precisely cross-dated to its year of formation, using standard

1 dendrochronological methods (Stokes and Smiley 1968). The sample size was five trees per year
2 and per elevation for $\delta^{13}\text{C}$ measurements with the exception of the dead trees at the Low site,
3 which had only four samples in 2002 due to missing rings.

4 After the increment cores had been cross-dated we split annual rings from each core
5 using a scalpel and a dissecting scope. We did not attempt to separate early- from late-wood
6 (Livingston and Spittlehouse 1996, Leavitt and Wright 2002) because our objective was to
7 examine crown-scale gas exchange at the annual time step. We did not extract cellulose prior to
8 measurement of $\delta^{13}\text{C}$ because numerous studies have reported constant relationships between
9 cellulose and whole-wood $\delta^{13}\text{C}$ for sapwood (Livingston and Spittlehouse 1996, Marshall and
10 Monserud 1996, Macfarlane et al. 1999, Warren et al. 2001, Loader et al. 2003, Harlow et al.
11 2006), and most cross-ring contamination is associated with carbon movement from the sapwood
12 into the heartwood (S. Leavitt *personal communication*) and all of our sample rings were located
13 within the sapwood. Each ring was individually diced and ground to a fine powder using a
14 mortar and pestle. The powder collected from each ring was analyzed on a Eurovector
15 Elemental Analyzer coupled to an Isoprime isotope ratio mass spectrometer (GV Instruments,
16 Manchester UK) operated in continuous flow mode at Los Alamos National Laboratory's Stable
17 Isotope Lab in Los Alamos, NM. Nitrous oxide was removed by gas chromatography and
18 corrections for ^{17}O (Craig 1957) were done for all runs. We ran 208 tree ring samples and
19 overall precision for $\delta^{13}\text{C}$ was 0.05‰ (n=52).

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

21
$$\Delta \approx \frac{\delta^{13}\text{C}_a - \delta^{13}\text{C}}{1 + \delta^{13}\text{C}} \quad (4).$$

1 We obtained annual atmospheric stable carbon isotope ratios ($\delta^{13}\text{C}_a$) from the Institute for Arctic
2 and Alpine Research (*INSTAAR*) at the University of Colorado and the National Oceanic and
3 Atmospheric Administration (*NOAA*), Earth System Research Laboratory (*ESRL*). Equation (4)
4 corrects for annual depletion of $\delta^{13}\text{C}_a$ associated with fossil fuel emissions of CO_2 depleted in
5 $\delta^{13}\text{C}$ (Leavitt and Long 1988, Keeling et al. 1989).

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

18 We were concerned about cross-contamination of $\delta^{13}\text{C}$ between rings during the process
19 of splitting the cores from trees at the Low site due to their particularly small rings. We
20 conducted a sensitivity analyses in which we regressed Δ versus climate variables (those shown
21 in Table 2) the following ways: 1) re-arrangement of Δ values for neighboring rings (e.g.,
22 swapping 1998 Δ with 1999 Δ) - this represents the most likely way contamination could occur;
23 2) using only Δ values for 1992-1999, the years prior to the particularly severe drought with the

1 particularly small rings; and 3) #2 repeated without cores that we noted had particularly small
2 rings. This analysis failed to generate any significant relationships (best r^2 and p-value were 0.09
3 and 0.31, respectively). In addition to this analysis, visual examination of the Δ results confirms
4 that even if carbon contaminated across rings, there is no ring that has Δ values sufficiently
5 negative to provide a significant regression of Δ or p_a-p_c vs. climate. We conclude that the $\delta^{13}\text{C}$
6 values for dead and live trees at the Low site are accurate, though signal attenuation remains a
7 concern.

8
9 ***Leaf nitrogen and specific leaf area*** Photosynthetic capacity and mesophyll conductance can
10 affect $\delta^{13}\text{C}$ interpretation because they can alter p_c without variation in g_s . Leaf nitrogen
11 concentration (N , %) and specific leaf area (SLA , $\text{cm}^2 \text{g}^{-1}$), respectively, are commonly used
12 metrics of these factors (e.g. Evans 1989, Evans et al. 1994, respectively, but see Warren et al.
13 2003), and may vary with elevation. It is currently impossible to quantify leaf N or SLA
14 retrospectively through tree rings (e.g. Hart and Classen 2003), so we sampled foliage from trees
15 at each site in June 2006 and assumed that N and SLA from this date were representative of the
16 relative differences between sites. We sampled foliage from the south aspect of the upper crown
17 third of each tree using an extendable pole pruner. Because all of the dendrometer banded trees
18 used for BAI and $\delta^{13}\text{C}$ at the Low site died in 2002, the only foliage samples from this site are
19 from the live trees. For the Mid and High sites we sampled the original dendrometer banded
20 trees. All sampling was done on the same day, and foliage was immediately returned to our
21 laboratory, stored in plastic bags in a refrigerator and measured the next day for leaf area.
22 Projected leaf area was determined using a LI-3100 Leaf Area Meter (Li-Cor, Lincoln, NE)
23 calibrated to 0.01 cm^2 (McDowell et al. 2008b). The foliage was then dried at 65°C until the

1 weight had stabilized to calculate the dry weight for *SLA*. Each foliage sample was ground to a
2 fine powder using a mortar and pestle, and leaf *N* was measured on a Vario Max CN macro
3 elemental analyzer (Elementar Analysensysteme GmbH, Hanau Germany).

4
5 ***Climatic response*** To test our hypothesis regarding climatic sensitivity we examined
6 relationships between *BAI*, *BAI/BA*, Δ and p_a-p_c with *PDSI*. We used instrumental *PDSI* data for
7 Climate Division 2 (northern mountains) of New Mexico, available from the National Climatic
8 Data Center (www.ncdc.noaa.gov). *PDSI* was used as the independent variable in regression
9 analysis. Our study period of 1992-2002 occurred at the transition from a ~20 year wet period
10 experienced by the region (1978-1995) into a dry period (post 1995). The years considered
11 severe “drought” years locally are 1996, 1998, 2000, 2001 and 2002. Wood growth in ponderosa
12 pine occurs during the spring and summer months, so in order to ensure that we were using *PDSI*
13 from the appropriate time period we conducted a correlation analyses of Δ , p_a-p_c , *BAI*, and
14 *BAI/BA* vs. *PDSI* from different time periods, including annual means, means of the previous
15 winter (October through March), and means of different periods during the spring and summer.
16 The strength of regressions did not exhibit a consistent dependency on which “growing season”
17 period was used. For all subsequent analyses of climate versus growth, Δ and p_a-p_c we use the
18 March-September time period because this period had slightly higher coefficients of
19 determination and because this time period encompasses the period of growth based on
20 dendrometer band measurements (Figure 3). There were no significant differences between
21 regressions using *BAI* and *BAI/BA*, or using Δ and p_a-p_c , so Table (2) and subsequent figures
22 show only regressions using *BAI/BA* and p_a-p_c .

1 Our *PDSI* values are specific to our study region but are not calculated for each specific
2 elevation. Therefore we also conducted correlation analyses using climate data from the nearest
3 meteorological stations to our specific sites. The three sites are located at 1996m, 2263m, and
4 3157m in elevation, and are within 1, 5, and 5 km of each of our study sites, respectively. These
5 sites are maintained by Bandelier National Monument and the Los Alamos National Laboratory
6 Meteorology Team (www.weather.lanl.gov). Climate characteristics including relative humidity
7 (R_h , %), vapor pressure deficit (*VPD*, kPa), precipitation (mm), air temperature (T_a , °C) and
8 *PDSI* were used (Table 2).

9
10 ***The Hydraulic Model*** We applied equation (2) in a similar fashion to Oren et al. (1999) and
11 McDowell et al. (2005, 2008b). Only *VPD*, Ψ_s and k_1 were allowed to vary in this modeling
12 exercise. We used growing season (April-September), elevation-specific *VPD* for the 11 years
13 of this study (1992-2002). We calculated Ψ_s as a relative function of elevation-specific
14 precipitation during the growing season. This is accomplished by dividing the maximum,
15 elevation-specific annual precipitation by each year's total precipitation. This resulted in values
16 for $\Psi_s - \Psi_1$ ranging between 0.35 (lowest precipitation) and 1.0 (highest precipitation) for each
17 site. We assumed that Ψ_1 is constant (isohydric) regardless of site water availability (Maherali
18 and Delucia 2001) and that k_1 is highest at the Low site (set to 1.0) and decreased 10% between
19 each successive higher elevation site (0.9 and 0.8 at the Mid and High sites, Maherali and
20 Delucia 2001). We allowed k_1 to decline with drought at variable rates for each site (Maherali et
21 al. 2002); however, this did not significantly alter the results so for simplicity we only present the
22 results with k_1 constant over time. To examine the role of k_1 in tree mortality, we varied k_1 in 0.01
23 increments for the dead trees and examined the fit of the regression of modeled g_s versus

1 observed p_a-p_c (the regression included all sites). The rationale for this analysis stemmed from
2 our absolute lack of knowledge of k_1 in dead trees and because k_1 integrates many hydraulic
3 parameters (e.g. leaf area:sapwood area ratio, rooting depth, sapwood permeability) that may
4 vary between live and dead trees.

5
6 **Results *Climate*** A summary of climate characteristics for the elevation-specific meteorological
7 stations during the study period of 1992-2002 is shown in Table (1). The Low, Mid, and High
8 elevation sites exhibited the expected differences in climate, with the Low site being the warmest
9 and driest and the High site the coolest and wettest. All comparisons in Table (1) had significant
10 differences between elevations ($p<0.05$) except basal area between Mid and High ($p=0.21$).

11
12 ***Intra-annual growth*** Figure (3a) shows weekly cumulative *BAI* averaged for the five wettest
13 years and five driest years. Figure (3b) shows the relative growth differential calculated as:
14 (mean *BAI* wet – mean *BAI* dry)/maximum *BAI*, which is an index of the response of *BAI* to
15 climate. Growth started in mid-April for the High and Mid sites for both wet and dry years
16 (Figure 3a). Growth at the Low site preceded the High and Mid sites by one or two weeks in wet
17 years. Low site growth was delayed until early July in dry years, though pin scar measurements
18 indicate cell division occurred in April and went undetected by dendrometer bands, perhaps due
19 to dehydration-induced stem shrinkage (C.D. Allen, unpublished data). Growth ended one or
20 two weeks earlier in dry years than wet years, and ended earlier at lower elevations. The
21 climatic dependency of growth clearly increased as site elevation decreased (Figure 3b). Note
22 that High site growth declined in only the two driest years (2001-2002) of the five “dry” years,
23 resulting in larger error bars for the High site in Figure (3a).

1
2 **Inter-annual growth and gas exchange PDSI** and growth generally decreased over the study
3 period (Figure 4A,B). Throughout the study period, *BAI/BA* of live trees was greater at higher
4 elevations (Figure 4B, Table 3, $p=0.01$). Low site dead trees had higher *BAI/BA* than Low site
5 live trees until the final two years of the study ($p<0.01$). p_a-p_c increased with decreasing site
6 elevation ($p=0.01$ for all years), and was slightly lower for dead than live trees at the Low site
7 (though not significantly, $p>0.10$, Table 3, Figure 4C). Δ exhibited similar patterns to p_a-p_c
8 (Table 3). Notably, the range of p_a-p_c values was smallest for trees that died, and increased with
9 elevation for live trees (Table 3).

10
11 **Climate sensitivity** Climate variables generally correlated well with p_a-p_c and growth except in
12 the case of trees that died, which showed no p_a-p_c correlation with climate (Table 2). p_a-p_c
13 showed increasing climate dependency with increasing elevation, as indicated by the coefficients
14 of determination. *PDSI* and *VPD* generally had the strongest fit statistics across all elevations. Δ
15 exhibited similar coefficients with climate as p_a-p_c (data not shown).

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

21 In stark contrast to growth, the climate sensitivity of p_a-p_c diverged between live and
22 dead trees (Figure 5B). There was no significant relationship between p_a-p_c and *PDSI* for trees
23 that died ($p>0.10$). There was a significant slope between p_a-p_c and *PDSI* for trees that survived

1 at each site ($p < 0.01$ for all three elevations). These slopes were similar for all three elevations
2 ($p > 0.10$). Similar results were observed for Δ (data not shown). The W:D analyses were
3 consistent with the slope tests, with limited sensitivity of $p_a - p_c$ ($p = 0.11$) and Δ ($p = 0.19$) to *PDSI*
4 for trees that died (W:D values near 1.0), whereas trees that survived at each site exhibited W:D
5 values of $p_a - p_c$ and Δ significantly different than 1.0 ($p < 0.01$, Table 3).

6
7 ***Dependence of growth on gas exchange*** All trees exhibited significant slopes of the relationship
8 between growth and $p_a - p_c$ ($p < 0.01$ for all live trees, $p = 0.03$ for dead trees, Figure 6). This slope
9 was similar for trees that survived at all three elevations regardless of whether *BAI* or *BAI/BA*
10 was utilized as the measure of growth ($p < 0.01$). In contrast, the slope of this relationship was
11 significantly steeper for trees that died at the Low site ($p = < 0.01$, Figure 6).

12
13 ***Leaf characteristics*** *SLA* must decrease and leaf *N* must increase with decreasing elevation for
14 either of these variables to confound the interpretation of $p_a - p_c$ as an index of g_s . *SLA* was not
15 different between the Low and Mid sites, but was lower at the High site ($p = 0.02$, Table 3). This
16 indicates that g_m may have been lower at the High site than the other two sites. Leaf *N* per gram
17 dry matter and per unit leaf area increased with elevation (Table 3), indicating that
18 photosynthetic capacity may have increased with increasing elevation. Thus, neither g_m nor
19 photosynthetic capacity appears to be the cause of the observed shifts in $p_a - p_c$. Instead, these
20 patterns suggest the isotopic shifts with elevation are an even stronger metric of g_s because they
21 would force $p_a - p_c$ in the opposite elevation trend than observed.

22

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

9 Modeled g_s strongly corroborated the empirical $p_a - p_c$ results (Figure 8). For live trees
10 only, the regression equation was: $p_a - p_c = -0.110 * g_s + 1.83$, $p < 0.001$, $r^2 = 0.76$. For trees that
11 died during the drought, we varied the k_1 parameterization of modeled g_s (equation 2) until we
12 obtained the highest regression fit within Figure (8) to assess the likely relative ranking of k_1 for
13 live versus dead trees. The highest fit of g_s to $p_a - p_c$ using all live and dead trees was found when
14 k_1 of dead trees was set to 0.65 at the low site ($p_a - p_c = -0.113 * g_s + 1.85$, $p < 0.001$, $r^2 = 0.77$). For
15 comparison, k_1 was 1.0, 0.9 and 0.8 for the live Low, Mid and High sites, respectively.

16
17 **Discussion** Building on the widespread observations of enhanced growth-sensitivity to climate
18 in trees that die, we proposed that if carbon starvation drives mortality (McDowell et al. 2008a),
19 and if gas exchange and growth are directly linked, then gas exchange should be more steeply
20 coupled to climate, i.e. more sensitive, in trees that die than trees that survive. We tested this
21 idea via three linked hypotheses. Our first hypothesis was supported; mortality was associated
22 with greater growth sensitivity to climate (Figure 5A, Table 3), which is consistent with
23 published observations. Our second hypothesis was refuted; mortality was not associated with

1 greater sensitivity of p_a-p_c to climate. Unlike the surviving trees, which showed a strong climatic
2 sensitivity of gas exchange, there was no apparent response of p_a-p_c to *PDSI* for trees that died
3 (Figure 5B, Table 3). Our third hypothesis, that variation in growth was correlated with p_a-p_c ,
4 was supported for all live and dead trees at all three elevations, with the steepest relationship for
5 trees that died (Figure 6). The dead trees' steep relationship between p_a-p_c and growth
6 concurrent with their insensitivity of p_a-p_c to climate requires a revised interpretation of the cause
7 of mortality. We hypothesize that carbon starvation remains a predisposing mechanism of
8 vulnerability to bark beetle attack, but that it occurred due in part to chronic water stress and a
9 subsequently narrow range of gas exchange (Figure 5-7, Table 3).

10

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

20 That trees that died had a narrower gas exchange range than neighboring trees that
21 survived indicates edaphic or within-tree constraints upon k_l . There were no obvious edaphic
22 differences between live and dead trees at low elevation. Stand density and shading were
23 similarly low for both (Figure 2, Table 1), and there were no apparent differences in aspect, soil

1 depth, or pathogen load. One clear within-tree difference is their size and structure - trees that
2 died had smaller basal areas (average basal areas of 918 and 1751 cm², respectively, $p < 0.001$)
3 but were the same height (Table 3, $p > 0.10$), and thus had greater ratios of height/BA (Table 3,
4 $p < 0.001$). Trees with lower basal areas and a greater height/BA ratio may have lower k_1 due to
5 shallower or less distributed rooting distribution (Dawson 1996, Meier and Leuschner 2008),
6 reduced sapwood area (Maherali and Delucia 2001), high leaf area:sapwood area ratios relative
7 to soil water availability (McDowell et al. 2006), or less capacitance (Phillips et al. 2003, Ryan et
8 al. 2006). Results of our model sensitivity analysis are consistent with this interpretation,
9 suggesting that dead trees may have had 35% lower k_1 than live trees (Figure 8) at the same
10 elevation. This interpretation is logical because k_1 integrates the hydraulic bottlenecks within the
11 tree and soil (Sperry et al. 2002), and thus a constraint on maximum k_1 will produce a narrower
12 range of g_s and limited sensitivity to climate. In contrast, trees that survive at low elevations
13 should be those that maximize k_1 because ponderosa pine increases k_1 to cope with the greater
14 water deficits at lower elevations (Maherali and Delucia 2001, Maherali et al. 2002). Based on
15 these empirical and theoretical results, we hypothesize that chronic constraints upon k_1 and g_s are
16 predisposing factors to mortality during drought.

17 The steep coupling of gas exchange and growth (Figure 6) suggests that an additional
18 factor beyond chronically low g_s is responsible for the growth-sensitivity of trees that died
19 (Figure 5A and 6). Potential reasons include 1) dynamic changes in canopy leaf area, 2) water
20 stress constraints on symplastic metabolism, 3) reduced carbohydrate storage capacity, and 4)
21 hydraulic failure. 1) Leaf shedding occurs in response to drought (Tyree et al. 1993, Suarez et al.
22 2004, Hultine et al. 2006), which reduces whole-tree photosynthesis and stemwood growth with
23 minimal changes in Δ (McDowell et al. 2006). This would allow large changes to occur in

1 *BAI/BA* without concomitant changes in tree ring $\delta^{13}\text{C}$, consistent with observations of *Fagus*
2 *sylvatica* (Peñuelas et al. 2008). 2) Water stress constraints on symplastic carbon metabolism
3 could occur if cell expansion, division, and carbohydrate use are limited by water potential
4 (Körner 2003, Alves and Setter 2004, Woodruff et al. 2004, Ryan et al. 2006). In severe drought
5 conditions, trees with less favorable water status could cease both growth and resin production,
6 leading to a steep relationship between *BAI/BA* and g_s , and elevated vulnerability to pathogen
7 attack. 3) Reduced carbohydrate storage capacity has not been investigated in trees that die;
8 however, if their cellular or whole-tissue storage capacity is low, then the length of time a tree
9 can survive without positive net photosynthesis will be diminished and carbon starvation, or
10 cessation of resin production, will ensue sooner (McDowell et al. 2008a). Lastly, 4) hydraulic
11 failure may have occurred if g_s failed to regulate transpiration above its cavitation threshold
12 (Sperry et al. 2002, McDowell et al. 2008a). This is consistent with a lack of g_s sensitivity to
13 climate and has been empirically shown in seedlings (Brodribb and Cochard 2009) and shrubs
14 (Davis et al. 2002), but not in mature trees (Cinnirella et al. 2002). Other factors that may
15 exacerbate, or be exacerbated by, chronic water stress include transient reductions in g_m (Flexas
16 et al. 2004, Warren et al. 2004) photosynthetic capacity (Martin and Ruiz-Torres 1992, Escalona
17 et al. 1999, Parry et al. 2002) hydraulic conductance (Maherali et al. 2002, Meier and Leuschner
18 2008) and regional population dynamics of insects (Raffa et al. 2008). Insect presence was
19 ubiquitous at our low elevation site in 2002-2003, so the population dynamics at the regional
20 level *per se* cannot explain why some trees died and some survived at the low elevation site.

21 ***A note on elevation studies of tree ring $\delta^{13}\text{C}$*** It appears that elevation- $\delta^{13}\text{C}$ studies fall into two
22 groups: 1) those that sampled plants with access to perennial water sources, and thus factors such
23 as photosynthetic capacity and g_m dominated p_a-p_c (Vitousek et al. 1990, Körner et al. 1991,

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

11

12 **Conclusions and climate change implications** Ecotonal ponderosa pine trees that died during
13 drought had the greatest climatic sensitivity of growth (BAI/BA), the least climatic sensitivity of
14 gas exchange (p_a-p_c and modeled g_s), and the steepest coupling between growth and gas
15 exchange relative to trees that survived. In comparison, all live trees conformed to similar
16 climatic sensitivities and dependency of growth and gas exchange. It appears that chronic
17 hydraulic constraints on g_s result in an insufficient buffer between wet and dry periods, leaving
18 only a narrow margin between ponderosa pine survival and death at dry ecotones. This result is
19 consistent with carbon starvation as a mechanism of death, but does not eliminate nor identify
20 the contribution of other mechanisms that are directly or indirectly driven by hydraulic
21 constraints (McDowell et al. 2008a).

22 Global climate change projections show increasing mean and extreme temperatures,
23 along with consistent projections of increasing drought severity and frequency in many parts of

1 the world, particularly in mid-latitude regions (Lawford et al. 1993, Hanson and Weltzin 2000,
2 Rosenberg et al. 2003, Weltzin et al. 2003, Cook et al. 2004, McCabe et al. 2004, IPCC 2007,
3 Seager et al. 2007). Impacts of drought appear to outweigh the benefits of CO₂ fertilization on
4 tree growth and survival, particularly in the drier portions of species distributions (Martínez-
5 Vilalta et al. 2008, Peñuelas et al. 2008, this study). It appears likely that a hydraulic mechanism
6 underlies hydraulic failure, carbon starvation, or symplastic limitations, thus we can expect
7 continued forest mortality in dry, temperate regions if climate projections of increased water
8 stress are accurate. Greater understanding of the coupled hydraulic-carbon mechanisms of tree
9 mortality is needed to improve our ability to forecast climate-induced forest mortality.

10
11

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24
25

References

1
2 Adams HD, Kolb TE (2004) Drought responses of conifers in ecotone forests of northern
3 Arizona: tree ring growth and leaf $\delta^{13}\text{C}$. *Oecologia* 140:217-225
4
5 Allen, C.D. 1989. Changes in the Landscape of the Jemez Mountains, New Mexico. Ph.D.
6 dissertation, University of California, Berkeley, CA. 346 p
7
8 Allen CD (2007) Cross-scale interactions among forest dieback, fire, and erosion in northern
9 New Mexico landscapes. *Ecosystems* 10:797-808
10
11 Allen CD, Breshears DD (1998) Drought-induced shift of a forest woodland ecotone: rapid
12 landscape response to climate variation. *Proc Natl Acad Sci USA* 95:14839-14842
13
14 Allen CD, Breshears DD (2007) Meetings: Organized Oral Session on "Climate-Induced Forest
15 Dieback as an Emergent Global Phenomenon: Patterns, Mechanisms, and Projections", Annual
16 Meeting of Ecological Society of America, San Jose, California, 7 August 2007. *EOS*
17 88(47):504
18
19 Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T,
20 Rigling A, Breshears DD, Gonzales P, Hogg EH, Fensham R, Zhang Z, Castro J, Lim JH, Allard
21 G, Running SW, Semerci A, Cobb N. (2009) A Global Overview of Drought-Induced Forest
22 Mortality Reveals Emerging Climate Change Risks. *Forest Ecology and Management*, *in review*
23
24 Alves AAC, Setter TL. (2004) Response of cassava leaf area expansion to water deficit: cell
25 proliferation, cell expansion and delayed development. *Annals of Botany* 94: 605-613.
26
27 Amthor JS (2000) The McCree-de Wit-Penning de Vries-Thornley respiration paradigms: 30
28 years later. *Ann Bot* 86:1-20
29
30 Beckage B, Osborne B, Gavin DG, Pucko C, Siccama T, Perkins T (2008) A rapid upward shift
31 of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proc Natl*
32 *Acad Sci USA* 105:4197-4202
33
34 Bentz BJ, Logan J, MacMahon J, Allen CD, Ayres M, Berg E, Carroll A, Hansen M, Hicke J,
35 Joyce L, Macfarlane W, Munson S, Negrón J, Paine T, Powell J, Raffa K, Régnière J, Reid M,
36 Romme W, Seybold SJ, Six D, Tomback D, Vandygriff J, Veblen T, White M, Witcosky J,
37 Wood D (In press) Bark Beetle Outbreaks in Western North America: Causes and Consequences.
38 USDA Forest Service Special Report. University of Utah Press
39
40 Berg EE, Henry D, Fastie JB (2006) Spruce beetle outbreaks on the Kenai Peninsula, Alaska,
41 and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures
42 and regional differences in disturbance regimes. *For Ecol Manage* 227:219-232
43
44 Bigler C, Braker OU, Bugmann H, Dobbertin M, Rigling A (2006) Drought as an inciting
45 mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems* 9:330-343
46

1 Breshears DD, Allen CD (2002) The importance of rapid, disturbance-induced losses in carbon
2 management and sequestration. *Glob Ecol Biogeogr Lett* 11:1-15
3
4 Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens JH,
5 Floyd ML, Belnap J, Anderson JJ, Myers OB, Meyer CW (2005) Regional vegetation die-off in
6 response to global-change-type drought. *Proc Natl Acad Sci USA* 102:15144-15148
7
8 Brodribb TJ, Cochard H. (2009). Hydraulic failure defines the recovery and point of death in
9 water-stressed conifers *Plant Physiol.* 149: 575-584
10
11 Cinnirella S, Magnani F, Saracino A, Borghetti M (2002) Response of mature *Pinus laricio*
12 plantation to a three-year restriction of water supply: structural and functional acclimation to
13 drought. *Tree Physiol* 22:21-30
14
15 Cobb NS, Mopper S, Gehring CA, Caouette M, Christensen KM, Whitham TG (1997) Increased
16 moth herbivory associated with environmental stress of pinyon pine at local and regional levels.
17 *Oecologia* 190:389-397
18
19 Coley PD, Bryant JP, Chapin FS III (1985) Resource availability and plant antiherbivore
20 defense. *Science* 230:895-899
21
22 Condit R, Hubbell SP, Foster RB (1995) Mortality rates of 205 neotropical tree and shrub
23 species and the impact of a severe drought. *Ecol Monogr* 65:419-439
24
25 Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW (2004) Long-term aridity changes
26 in the western United States. *Science* 306 (5698):1015-1018
27
28 Coops NC, Waring RH, Law BE (2005) Assessing the past and future distribution and
29 productivity of ponderosa pine in the Pacific Northwest using a process model, 3-PG. *Ecol*
30 *Modell* 183:107-124
31
32 Cordell S, Goldstein G, Meinzer FC, Handley LL (1999) Allocation of nitrogen and carbon in
33 leaves of *Metrosideros polymorpha* regulates carboxylation capacity and $\delta^{13}\text{C}$ along an
34 altitudinal gradient. *Functional Ecology* 13:811-818
35
36 Craig H (1957) Isotopic standards for carbon and oxygen and correction factors for mass-
37 spectrometric analysis of carbon dioxide. *Geochim Cosmochim Acta* 12:133-149
38
39 Davis SD, Ewers FW, Sperry JS, Portwood KA, Crocker MC, Adams GC (2002) Shoot dieback
40 during prolonged drought in *Ceanothus* (Rhamnaceae) chaparral of California: a possible case of
41 hydraulic failure. *Am J Bot* 89:820-828
42
43 Dawson TE (1996) Determining water use by trees and forests from isotopic, energy balance and
44 transpiration analyses: the role of tree size and hydraulic lift. *Tree Physiology* 16:263-272.
45

- 1 Demchik MC, Sharpe WE (2000) The effect of soil nutrition, soil acidity and drought on
2 northern red oak (*Quercus rubra* L.) growth and nutrition on Pennsylvania sites with high and
3 low red oak mortality. For Ecol Manage 136:199-207
4
- 5 Ehleringer JR, Hall AE, Farquhar GD (1993) Carbon and water relations in desert plants: an
6 isotopic perspective. Stable isotopes and plant carbon-water relations. Academic Press, Inc, San
7 Diego
8
- 9 Escalona JM, Flexas J, Medrano H (1999) Stomatal and non-stomatal limitations of
10 photosynthesis under water stress in field-grown grapevines. Aust J Plant Physiol 26:421-433
11
- 12 Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C3 plants. Oecologia
13 78:9-19
14
- 15 Evans JR, von Caemmerer S, Setchell BA, Hudson GS (1994) The relationship between CO₂
16 transfer conductance and leaf anatomy in transgenic tobacco with a reduced content of Rubisco.
17 Aust J Plant Physiol 21:475-495
18
- 19 Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO₂
20 assimilation in leaves of C₃ species. Planta 149:78-90
21
- 22 Farquhar GD, O'leary MH, Berry JA (1982) On the relationship between carbon isotope
23 discrimination and intercellular carbon dioxide concentration in leaves. Aust J Plant Physiol
24 9:121-137
25
- 26 Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and
27 photosynthesis. Annu Rev Plant Physiol Plant Mol Biol 40:503-537
28
- 29 Fensham RJ, Holman JE (1999) Temporal and spatial patterns in drought-related tree dieback in
30 Australian savanna. J Appl Ecol 36:1035-1060
31
- 32 Fensham RJ, Fairfax RJ, Ward DP (2009) Drought-induced tree death in savanna. Gobar Change
33 Biol. 15: 380-387
34
- 35 Flexas J, Bota J, Loreto F, Cornic G, Sharkey TD (2004) Diffusive and metabolic limitations to
36 photosynthesis under drought and salinity in C-3 plants. Plant Biol 6:269-279
37
- 38 Francey RJ, Farquhar GD (1982) An explanation of ¹³C/¹²C variations in tree rings. Nature
39 297:28-31
- 40 Gaylord, ML, TE Kolb, KF Wallin, MR Wagner. 2007. Seasonal dynamics of tree growth,
41 physiology and resin defenses in a northern Arizona ponderosa pine forest. Canadian Journal of
42 Forest Research *In press*.
43
- 44 Gitlin AR, Stultz CM, Bowker MA, Stumpf S, Ecton K, Kennedy K, Monoz A, Bailey JK,
45 Whitham TG (2006) Mortality gradients within and among dominant plant populations as
46 barometers of ecosystem change during extreme drought. Conserv Biol 20:1477-1486

1
2 Gonzalez P (2001) Desertification and a shift of forest species in the West African Sahel. *Clim*
3 *Res* 17:217-228
4
5 Hanson PJ, Weltzin JF (2000) Drought disturbance from climate change: response of United
6 States forests. *Sci Total Environ* 262:205-220
7
8 Harlow, BA, Marshall JD, Robinson AP. 2006. A multi-species comparison of $\delta^{13}\text{C}$ from whole
9 wood, extractive-free wood, and holocellulose. *Tree. Physiol.* 26: 767-774.
10
11 Hart SC, Classen AT (2003) Potential for assessing long-term dynamics in soil nitrogen
12 availability from variations in $\delta^{15}\text{N}$ of tree rings. *Isotopes Environ Health Stud* 39:15-28
13
14 Hultine KR, Marshall JD (2000) Altitude trends in conifer leaf morphology and stable isotope
15 composition. *Oecologia* 123:32-40
16
17 Hultine KR, Koepk DF, Pockman WT, Fravolini A, Sperry JS, Williams DG (2006) Influence of
18 soil texture on hydraulic properties and water relations of a dominant warm-desert phreatophyte.
19 *Tree Physiol* 26:313-323
20
21 IPCC, 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working*
22 *Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change,*
23 *IPCC Secretariat, Geneva Switzerland.*
24
25 Keeling CD, Bacastow RB, Carter AF, Piper SC, Whorf TP, Heimann M, Mook WG, Roeloffzen
26 (1989) A three-dimensional model of atmospheric CO_2 transport based on observed winds. 1.
27 Analysis of observational data. *in* D.H. Peterson, editor, *Geophysical Monographs, American*
28 *Geophysical Union* 55:165-236
29
30 Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent
31 climate change. *Proc Natl Acad Sci USA* 105:11823-11826
32
33 Kogami H, Hanba YT, Kibe T, Terashima I, Masuzawa T (2001) CO_2 transfer conductance, leaf
34 structure and carbon isotope composition of *Polygonum cuspidatum* leaves from low and high
35 altitudes. *Plant Cell Environ* 24:529-538
36
37 Körner C, Farquhar GD, Wong SC (1991) Carbon isotope discrimination follows latitudinal and
38 altitudinal trends. *Oecologia* 88:30-40
39
40 Körner C. (2003) Tansley Lecture: Carbon limitation in trees. *Journal of Ecology*, 91: 4-17.
41
42 Körner C. (2007) The use of 'altitude' in ecological research. *Trends in Ecol. and Evol.* 22: 569-
43 574.
44
45 Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L.
46 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452: 987-990.

1
2 Lajtha K, Getz J (1993) Photosynthesis and water use efficiency in pinyon-juniper communities
3 along an elevation gradient in northern New Mexico. *Oecologia* 94:95-111
4
5 Lawford RG, Mooney HA, Fuentes ER, Kronberg BI (1993) Regional hydrologic responses to
6 climate change in western North America. *Earth system response to global change*. Academic
7 Press, San Diego
8
9 Leavitt SW, Long A (1988) Stable carbon isotope chronologies from trees in the southwestern
10 United States. *Global Biogeochem Cycles* 2:189-198
11
12 Leavitt SW, Wright WE (2002) Spatial expression of *ENSO*, drought, and summer monsoon in
13 seasonal $\delta^{13}\text{C}$ of ponderosa pine tree rings in southern Arizona and New Mexico. *J Geophys Res*
14 107:1-10
15
16 Li CY, Liu SR, Berninger F (2004) *Picea* seedlings show apparent acclimation to drought with
17 increasing altitude in the eastern Himalaya. *Trees - Struct Funct* 18:277-283
18
19 Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. *Glob Chang*
20 *Biol* 13: 2089-2109
21
22 Livingston NJ, Spittlehouse DL (1996) Carbon isotope fractionation in tree ring early and late
23 wood in relation to intra-growing season water balance. *Plant Cell Environ* 19:768-774
24
25 Loader NJ, Robertson I, McCarroll D (2003) Comparisons of stable carbon isotope ratios in the
26 whole-wood, cellulose and lignin of oak tree-rings. *Palaeogeogr Palaeoclimatol Palaeoecol*
27 196:394-407
28
29 Macfarlane C, Warren CR, White DA, Adams MA (1999) A rapid and simple method for
30 processing wood to crude cellulose for analysis of stable carbon isotopes in tree rings. *Tree*
31 *Physiol* 19:831-835
32
33 Maherali H, DeLucia EH (2001) Influence of climate-driven shifts in biomass allocation on
34 water transport and storage in ponderosa pine. *Oecologia* 129:481-491
35
36 Maherali H, Williams BL, Paige KN, Delucia EH (2002) Hydraulic differentiation of ponderosa
37 pine populations along a climate gradient is not associated with ecotypic divergence. *Funct Ecol*
38 16:510-521
39
40 Manion PD (1981) *Tree Disease Concepts*, 2nd ed. Prentice Hall, New Jersey
41
42 Marshall, JD, Waring RH. 1985. Predicting fine root production and turnover by monitoring
43 root starch and soil temperature. *Can. J. For. Res.* 15:791-800.
44
45 Marshall JD, Zhang J (1994) Carbon isotope discrimination and water use efficiency of native
46 plants in the North-Central Rockies. *Ecology* 75:1887-1895

1
2 Marshall JD, Monserud RA (1996) Homeostatic gas-exchange parameters inferred from $^{13}\text{C}/^{12}\text{C}$
3 in tree rings of conifers. *Oecologia* 105:13-21
4
5 Martin B, Ruiz-Torres NA (1992) Effects of water-deficit stress on photosynthesis, its
6 components and component limitations, and on water use efficiency in wheat (*Triticum aestivum*
7 L.) *Plant Physiol* 100:733-739
8
9 Martínez-Vilalta J, López BC, Adell N, Badiella L, Ninyerola M (2008) Twentieth century
10 increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Global*
11 *Change Biology* 14: 1-14
12
13 McCabe GJ, Palecki MA, Betancourt JL (2004) Pacific and Atlantic Ocean influences on multi-
14 decadal drought frequency in the United States. *Proc Natl Acad Sci* 101:4136-4141
15
16 McDowell NG, Licata J, Bond BJ (2005) Environmental sensitivity of gas exchange parameters
17 in different-sized trees. *Oecologia* 145:9-20
18
19 McDowell NG, Adams HA, Bailey JD, Hess M, Kolb TE (2006) Homeostatic maintenance of
20 ponderosa pine gas exchange in response to stand density changes. *Ecol Appl* 16(3):1164-1182
21
22 McDowell NG, Adams HD, Bailey JD, Kolb TE (2007) The role of stand density on growth
23 efficiency, leaf area index and resin flow in southwestern ponderosa pine forests. *Canadian*
24 *Journal of Forest Research*, 37: 343-355.
25
26 McDowell NG, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb TK, Plaut J, Sperry J,
27 West A, Williams D, Yopez EA. (2008a) Tansley Review: Mechanisms of plant survival and
28 mortality during drought: Why do some plants survive while others succumb to drought? *New*
29 *Phytologist*, 178: 719-739.
30
31 McDowell NG, White S, Pockman WT. (2008b). Transpiration and stomatal conductance across
32 a steep climate gradient in the southern Rocky Mountains. *Ecohydrology*, 1:193-204.
33
34 Meier IC, Leuschner C. 2008. Belowground drought response of European beech: fine root
35 biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Global*
36 *Change Biology* 14: 2081-2095.
37
38 Natural Resource Conservation Service (2007) A soil survey of Bandelier National Monument,
39 New Mexico. US Dept of Agriculture, Denver, CO, USA (in press)
40
41 Newman BD, Wilcox BP, Archer SR, Breshears DD, Dahm CN, Duffy CJ, McDowell NG,
42 Phillips FM, Scanlon BR, Vivoni ER (2006) Ecohydrology of water-limited environments: a
43 scientific vision. *Water Resour Res* 42, W06302 DOI 10.1029/2005WR004141
44
45 Ogle K, Whitham TG, Cobb NS (2000) Tree-ring variation in pinyon predicts likelihood of death
46 following severe drought. *Ecology* 81:3237-3243

1
2 Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schäfer K VR (1999) Survey
3 and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure
4 deficit. *Plant Cell and Environ* 22: 1515-1526.
5
6 Orvis KH, Grissino-Mayer HD (2002) Standardizing the reporting of abrasive papers used to
7 surface tree-ring samples. *Tree-Ring Res* 58:47-50
8 Palmer WC (1965) Meteorological drought. Res Pap #45, U.S. Weather Bureau, Washington
9 D.C.
10
11 Pate JS 2001. Carbon isotope discrimination and plant water-use efficiency. In: Unkovich M,
12 Pate JS, McNeill A, Gibbs DJ (eds) *Stable Isotope Techniques in the Study of Biological*
13 *Processes and Functioning of Ecosystems*. Kluwer, Boston, pp 19-36.
14
15 Parry MAJ, Adralojc PJ, Khan S, Lea PJ, Keys AJ (2002) Rubisco activity: effects of drought
16 stress. *Ann Bot* 89:833-829
17
18 Pedersen BS (1998) The role of stress in the mortality of midwestern oaks as indicated by growth
19 prior to death. *Ecology* 79:79-93
20
21 Peñuelas J, Hunt JM, Ogaya R, Jump AS. (2008) Twentieth century changes of tree-ring $\delta^{13}\text{C}$ at
22 the southern range-edge of *Fagus sylvatica*: increasing water-use efficiency does not avoid the
23 growth decline induced by warming at low altitudes. *Global Change Biology* 14: 1076-1088.
24
25 Phillips N, Bond BJ, McDowell NG, Ryan MG (2002) Canopy and hydraulic conductance in
26 young, mature and old Douglas-fir trees. *Tree Physiol* 22:205-211
27
28 Phillips N, Ryan MG, Bond BJ, McDowell NG, Hinckley TM, Cermak J. (2003) Reliance on
29 stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiol*
30 23:237-245.
31
32 Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008.
33 Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics
34 of bark beetle eruptions. *Bioscience* 58: 501-517.
35
36 Rosenberg NJ, Brown RA, Izaurralde RC, Thomson AM (2003) Integrated assessment of the
37 Hadley Centre (HadCM2) climate change projections on agricultural productivity and irrigation
38 water supply in the conterminous United States I. Climate change scenarios and impacts on
39 irrigation water supply simulated with the HUMUS model. *Agric For Meteorol* 117:73-96
40
41 Ryan MG, Gower ST, Hubbard RM, Waring RH, Gholz HL, Cropper WP Jr, Running SW
42 (1995) Woody tissue maintenance respiration of four conifers in contrasting climates. *Oecologia*
43 101:133-140
44
45 Ryan MG, Phillips N, Bond BJ. (2006) The hydraulic limitation hypothesis revisited. *Plant,*
46 *Cell and Environment* 29: 367-381.

1
2 Saurer M, Siegwolf RTW, Schweingruber FH. 2004. Carbon isotope discrimination indicates
3 improving water-use efficiency of trees in northern Eurasia over the last 100 years. *Global*
4 *Change Biology* 10: 2109-2120.
5
6 Seibt U, Rajabi A, Griffiths H, Berry JA. (2008) Carbon isotopes and water use efficiency -
7 sense and sensitivity. *Oecologia* 155, 441-454. doi: 10.1007/s00442-007-0932-7.
8 Shaw JD, Steed BE, DeBlander LT (2005) Forest Inventory and Analysis (FIA) annual inventory
9 answers the question: what is happening to pinyon-juniper woodlands? *J For* 103:280-285
10
11 Sparks JP, Ehleringer JR (1997) Leaf carbon isotope discrimination and nitrogen content for
12 riparian trees along elevation transects. *Oecologia* 109:362-367
13
14 Sperry J, Hacke U, Oren R, Comstock J (2002) Water deficits and hydraulic limits to leaf water
15 supply. *Plant Cell Environ* 25:251-263
16
17 Stokes MA, Smiley TL (1968) An introduction to tree-ring dating. The University of Chicago
18 Press, Chicago.
19
20 Suarez ML, Ghermandi L, Kitzberger T (2004) Factors predisposing episodic drought-induced
21 tree mortality in *Nothofagus* – site, climatic sensitivity, and growth trends. *J Ecol* 92:954-966
22
23 Swetnam TW, Betancourt JL (1998) Mesoscale disturbance and ecological response to decadal
24 climatic variability in the American Southwest. *J Clim* 11:3128-3147
25
26 Tang K, Feng X, Funkhauser G. (1999). The $\delta^{13}\text{C}$ of tree rings in full-bark and strip-bark
27 bristlecone pine trees in the White Mountains of California. *Global Change Biology* 5: 33-40.
28
29 Treydte K, Schleser GH, Schweingruber FH, Winiger M (2001) The climatic significance of
30 $\delta^{13}\text{C}$ in subalpine spruces (Lötschental, Swiss Alps). *Tellus* 53B:593-611
31
32 Tyree MT, Cochard H, Cruiziat P, Sinclair B, Ameglio T (1993) Drought-induced leaf shedding
33 in walnut: evidence for vulnerability segmentation. *Plant Cell Environ* 16:879-882
34
35 Van de Water PK, Leavitt SW, Betancourt JL (2002) Leaf $\delta^{13}\text{C}$ variability with elevation, slope,
36 aspect and precipitation in the southwest United States. *Oecologia* 132:332-343
37
38 van Mantgem PJ, Stephenson NL (2007) Apparent climatically-induced increase of tree
39 mortality rates in a temperate forest. *Ecology Letters* 10:909-916
40
41 van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fulé PZ, Harmon ME,
42 Larson AJ, Smith JM, Taylor AH, Veblen TT (2009). Widespread increase of tree mortality rates
43 in the western United States. *Science*. 323: 521-524.
44
45 Vitousek PM, Field CB, Matson PA (1990) Variation in foliar $\delta^{13}\text{C}$ in Hawaiian *Metrosideros*
46 *polymorpha*: a case of internal resistance? *Oecologia* 84:362-370

1
2 Walcroft AS, Silvester WB, Whitehead D, Kelliher FM (1997) Seasonal changes in stable carbon
3 isotope ratios within annual rings of *Pinus radiata* reflect environmental regulation of growth
4 processes. *Aust J Plant Physiol* 24:57-68
5
6 Wallin, KF, TE Kolb, K Skov, MR Wagner. 2003. Effects of crown scorch on ponderosa pine
7 resistance to bark beetles in northern Arizona. *Environmental Entomology* 32:652-661.
8
9 Waring RH (1987) Characteristics of trees predisposed to die. *Bioscience* 37(8):569-577
10
11 Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forests: a constant
12 fraction of gross primary production? *Tree Physiol* 18:129-134
13
14 Waring RH, Law BJ. (2001) The ponderosa pine ecosystems and environmental stress: past,
15 present and future. *Tree Physiology*, 21: 273-274.
16
17 Warren CR, McGrath JF, Adams MA (2001) Water availability and carbon isotope
18 discrimination in conifers. *Oecologia* 127:476-486
19
20 Warren CR, Ethier GJ, Livingston NJ, Grant NJ, Turpin DH, Harrison DL, Black TA (2003)
21 Transfer conductance in second growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)
22 canopies. *Plant Cell Environ* 26:1215-1227
23
24 Warren CR, Livingston NJ, Turpin DH (2004) Water stress decreases the transfer conductance of
25 Douglas-fir (*Pseudotsuga menziesii*) seedlings. *Tree Physiol* 24:971-979
26
27 Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE,
28 Knapp AK, Lin G, Pockman WT, Shaw MR, Small E, Smith MD, Tissue DT, Zak J (2003)
29 Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience*
30 53:1-12
31
32 Whitehead D, Edwards WRN, Jarvis PG (1984) Conducting sapwood area, foliage area, and
33 permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. *Can J For Res* 14:940-947.
34
35 Whitehead D (1998) Regulation of stomatal conductance and transpiration in forest canopies.
36 *Tree Physiol.* 18:633-644.
37
38 Williams M, Bond BJ, Ryan MG (2001) Evaluating different soil and plant hydraulic constraints
39 on tree function using a model and water flux data from ponderosa pine. *Plant Cell and Environ*
40 24: 679-690.
41
42 Woodruff DR, Bond BJ, Meinzer FC. (2004) Does turgor limit growth in tall trees? *Plant Cell*
43 *and Environ*, 27: 229-236.

1 **Table 1:** Site characteristics including coordinates (latitude and longitude), elevation (m), stand
 2 density (live and dead, all species, all sizes) as # of trees per hectare and as basal area ($\text{m}^2 \text{ha}^{-1}$),
 3 and mean annual climate for the study period (1992-2002) including precipitation (mm),
 4 maximum and minimum temperature ($^{\circ}\text{C}$) and vapor pressure deficit (kPa) during daylight hours.
 5 Values in parentheses are standard errors of the 11 year means.

<i>Site</i>	<i>Low</i>	<i>Mid</i>	<i>High</i>
Coordinates	35°79', -106°27'	35°84', -106°40'	35°84', -106°36'
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 Precip (mm)	350 (23)	440 (30)	500 (31)
Max Temp. ($^{\circ}\text{C}$)	18.2 (0.2)	15.7 (0.2)	9.5 (0.2)
Min Temp. ($^{\circ}\text{C}$)	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)

6
7

1 **Table 2:** Coefficients of determination (r^2) for regressions between climate, p_a-p_c and BAI . The regressions were conducted to assess
2 the impact of using climate means from different time periods when examining climatic sensitivity. Time periods analyzed included
3 previous winter, May-August, March-September, April-July, and annual means, but the best fits were found for March-September so
4 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
5 only the results for BAI/BA . Parameters are defined in the Methods. Significant correlations at $\alpha= 0.05$ are bolded.

	Low-dead		Low-live		Mid		High	
Parameter	p_a-p_c	BAI/BA	p_a-p_c	BAI/BA	p_a-p_c	BAI/BA	p_a-p_c	BAI/BA
9 Min R_h	0.00	0.85	0.51	0.59	0.70	0.93	0.95	0.57
10 VPD	0.01	0.84	0.63	0.75	0.74	0.94	0.95	0.53
11 Precip	0.00	0.39	0.01	0.13	0.69	0.75	0.88	0.53
12 Min T_a	0.09	0.31	0.27	0.34	0.63	0.60	0.74	0.43
13 Max T_a	0.01	0.76	0.56	0.74	0.74	0.89	0.88	0.45
14 $PDSI$	0.00	0.86	0.48	0.87	0.73	0.85	0.84	0.48
15 Average	0.02	0.67	0.41	0.57	0.71	0.83	0.86	0.50

1 **Table 3:** Stand level mean values of BAI ($\text{cm}^2 \text{yr}^{-1}$), BAI/BA ($\text{cm}^2 \text{cm}^{-2} \text{yr}^{-1}$), Δ ($\%$), p_a-p_i (Pa),
2 the ratio of each of these for five wet versus five dry years (W:D), leaf nitrogen per unit dry
3 weight ($\%$) and per unit leaf area (g cm^{-2}), specific leaf area ($\text{cm}^2 \text{g}^{-1}$), tree height (m) and
4 height/BA (m/m^2). Dead trees lacked needles and could not be sampled for leaf characteristics.
5 Modeled g_s is calculated on a relative scale (see methods). Values in parentheses are standard
6 errors.

<i>Site</i>	<i>Low-dead</i>	<i>Low-live</i>	<i>Mid</i>	<i>High</i>
Mean <i>BAI</i>	11.76 (2.54)	13.93 (2.63)	17.34 (1.86)	32.56 (2.48)
Mean $BAI/BA * 10^3$	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 (<i>BAI</i>)	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	n/a	1.28 (0.10)	1.33 (0.03)	1.41 (0.03)
Leaf N	n/a	0.055 (0.001)	0.056 (0.001)	0.066 (0.002)
<i>SLA</i>	n/a	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)
Min. modeled g_s	0.08	0.12	0.14	0.23
Max. 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

1 **Figure captions**

2
3 **Figure 1.** Locations of High (H), Mid (M), and Low (L) live (circle) and dead (triangle) sites
4 along an elevation gradient in Bandelier National Monument, 12.2-meter (40-foot) contours
5 displayed. Shading indicates persistent forest (light grey), persistent woodland (white), and
6 ponderosa forest mortality zone (dark grey) from a previous severe drought in the 1950's
7 (mapped by Allen 1989, Allen and Breshears 1998), showing that the Low site is located at the
8 2002 forest/woodland ecotone. Extensive low-elevation ponderosa pine mortality in 2002-2003
9 caused this ecotone to shift further upslope (unmapped)

10
11 **Figure 2.** Low-elevation ponderosa pine trees that died in 2002-2003 near the Low site. The
12 surviving understory of *Juniperus monosperma* is typical of transition to woodland at such lower
13 ecotone sites.

14
15 **Figure 3. A.** Weekly basal area increment for the Low (dead), Mid, and High sites, averaged for
16 the five wet and five dry years (see Methods for years of averaging). Calendar months are
17 provided for reference. Bars are standard errors. **B.** The relative growth differential for each
18 site, calculated as: (mean *BAI* wet – mean *BAI* dry)/maximum *BAI*.

19
20 **Figure 4. A.** Mean annual *PDSI* for northern New Mexico for 1992-2002. Positive values of
21 *PDSI* are wet periods and negative values are dry periods. **B.** *BAI/BA* and **C.** p_a-p_c of trees at the
22 Low-dead, Low, Mid and High elevation sites for 1992-2002. Bars are standard errors.

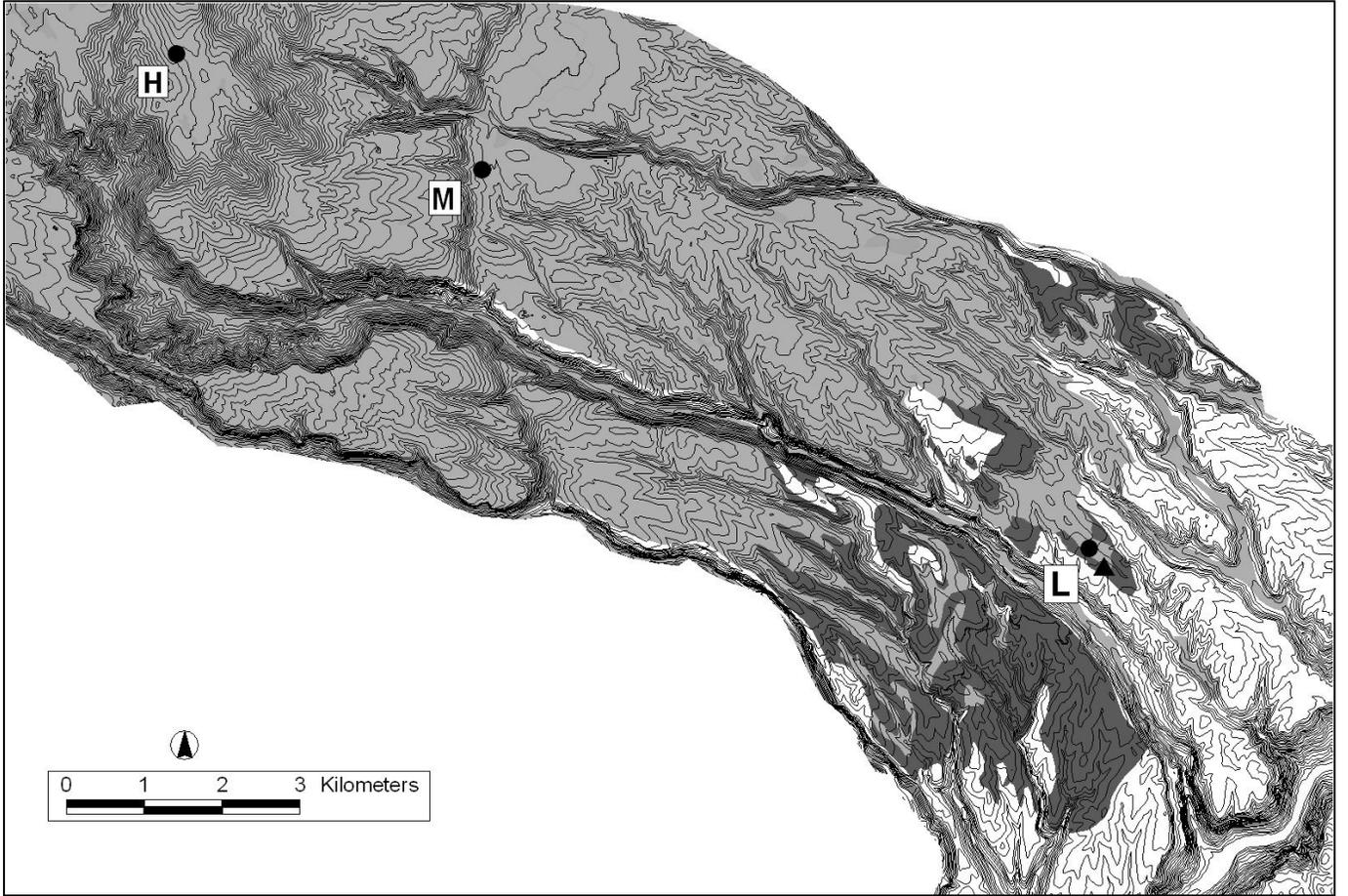
23
24 **Figure 5. A.** Mean annual *BAI/BA* versus *PDSI* for 1992-2002. The regression lines are: *BAI/BA*
25 (Low-dead) = $0.0028 * PDSI + 0.011$, $p < 0.01$, $r^2 = 0.85$ (dashed line), *BAI/BA* (Low) =
26 $0.0015 * PDSI + 0.007$, $p < 0.01$, $r^2 = 0.87$, *BAI/BA* (Mid) = $0.0018 * PDSI + 0.012$, $p < 0.01$, $r^2 = 0.83$,
27 *BAI/BA* (High) = $0.0020 * PDSI + 0.024$, $p < 0.05$, $r^2 = 0.49$. **(B)** Mean p_a-p_c versus growing season
28 *PDSI* (March-September) for 1992-2002. The regression lines are: p_a-p_c (Low) = $-0.26 * PDSI +$
29 14.7 , $p < 0.01$, $r^2 = 0.62$, p_a-p_c (Mid) = $-0.28 * PDSI + 13.24$, $p < 0.01$, $r^2 = 0.76$, and p_a-p_c (High) = -
30 $0.35 * PDSI + 11.71$, $p < 0.01$, $r^2 = 0.86$. There was no significant relationship for the Low-dead
31 site ($p = 0.23$, $r^2 = 0.16$, dashed line).

32
33 **Figure 6.** Mean *BAI/BA* versus p_a-p_c . The regression lines are *BAI/BA* (Low) = $-0.0059 * p_a-p_c +$
34 0.093 , $p < 0.01$, $r^2 = 0.87$, *BAI/BA* (Mid) = $-0.0054 * p_a-p_c + 0.085$, $p < 0.01$, $r^2 = 0.82$, and *BAI/BA*
35 (High) = $-0.0058 * p_a-p_c + 0.092$, $p < 0.01$, $r^2 = 0.59$. There was no significant relationship for the
36 Low-dead site ($p = 0.08$, $r^2 = 0.30$, dashed line).

37
38 **Figure 7.** Stomatal conductance modeled from equation (2) versus elevation-specific *VPD*. The
39 non-linear regression lines are: g_s (Low-dead) = $4.80e^{-1.35 * VPD}$, $p < 0.01$, $r^2 = 0.77$, g_s (Low) =
40 $5.99e^{-1.35 * VPD}$, $p < 0.01$, $r^2 = 0.77$, g_s (Mid) = $10.61e^{-1.84 * VPD}$, $p < 0.01$, $r^2 = 0.92$, and g_s (High) =
41 $6.84e^{-2.40 * VPD}$, $p < 0.01$, $r^2 = 0.96$.

42
43 **Figure 8.** p_a-p_c derived from tree ring $\delta^{13}C$ data versus modeled stomatal conductance from
44 equation (2). The regression line is: p_a-p_c (all sites) = $-0.113 * g_s + 1.85$, $p < 0.001$, $r^2 = 0.77$.

1 **Figure 1**



1 **Figure 2**



Figure 3

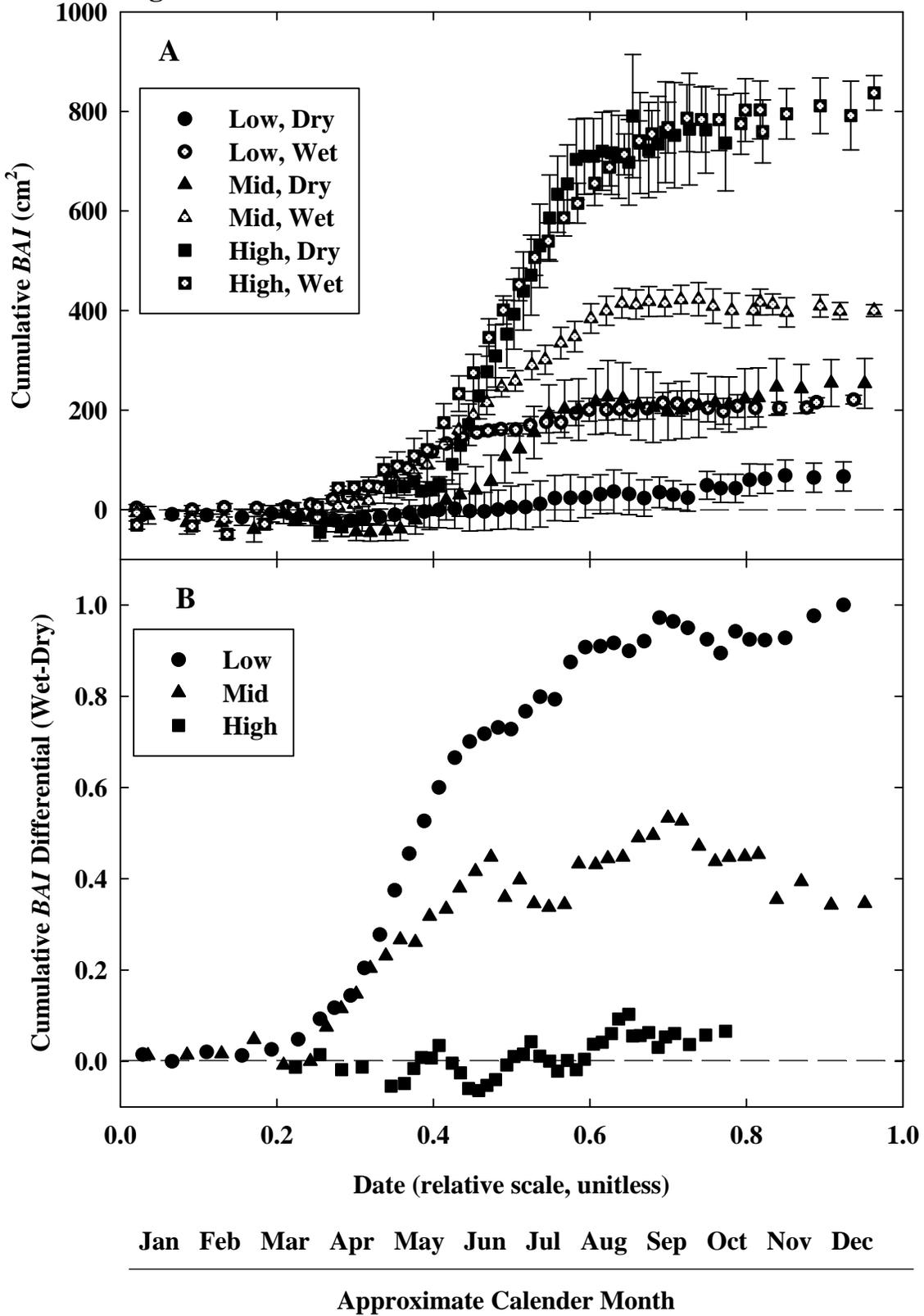


Figure 4

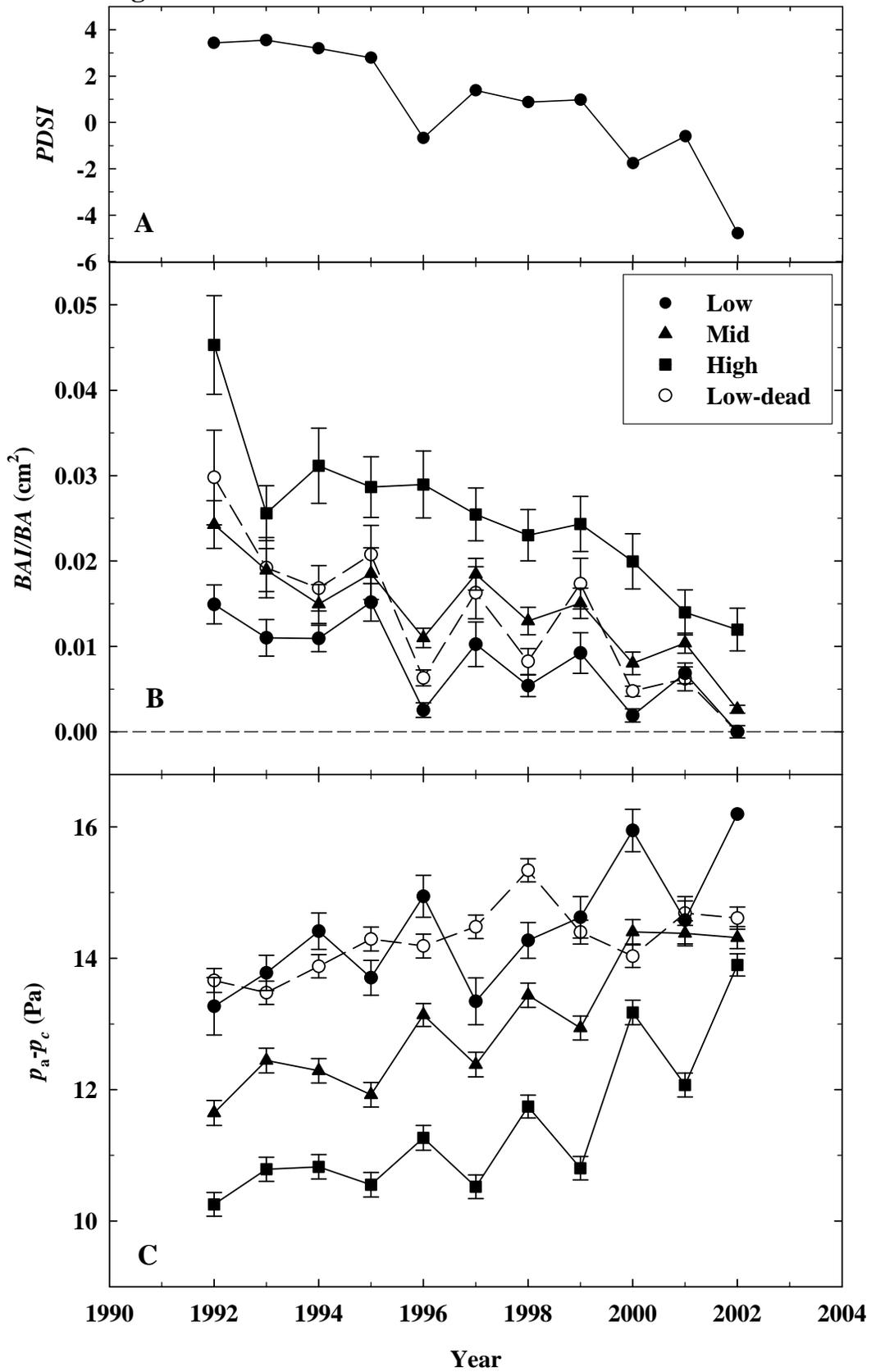
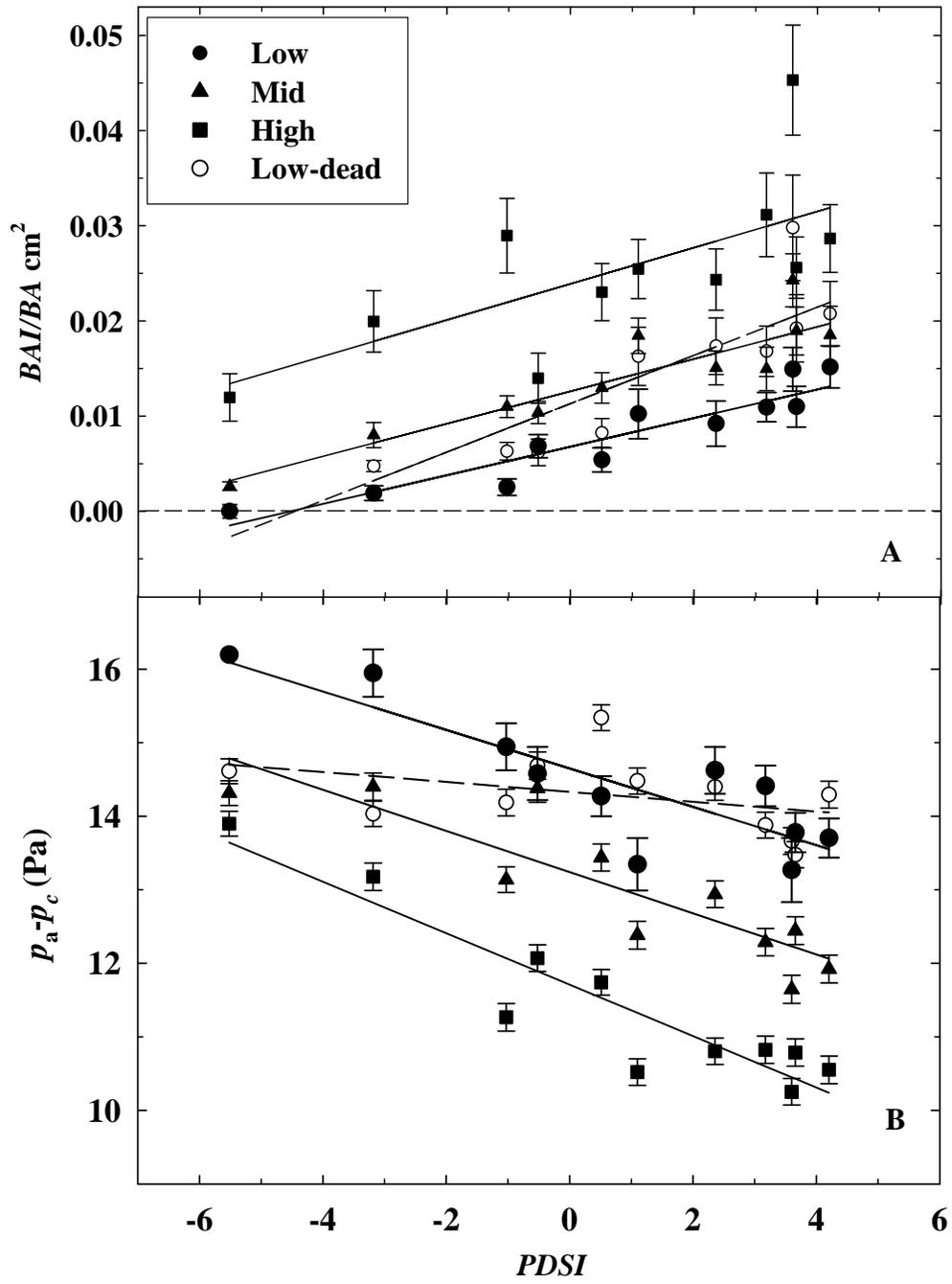
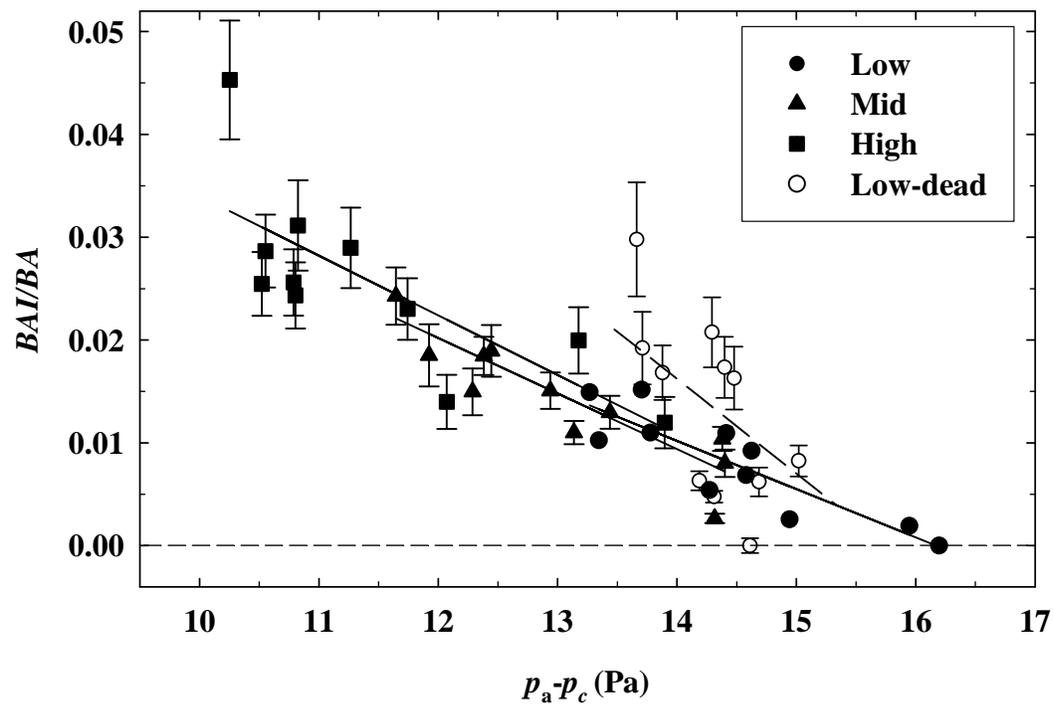


Figure 5



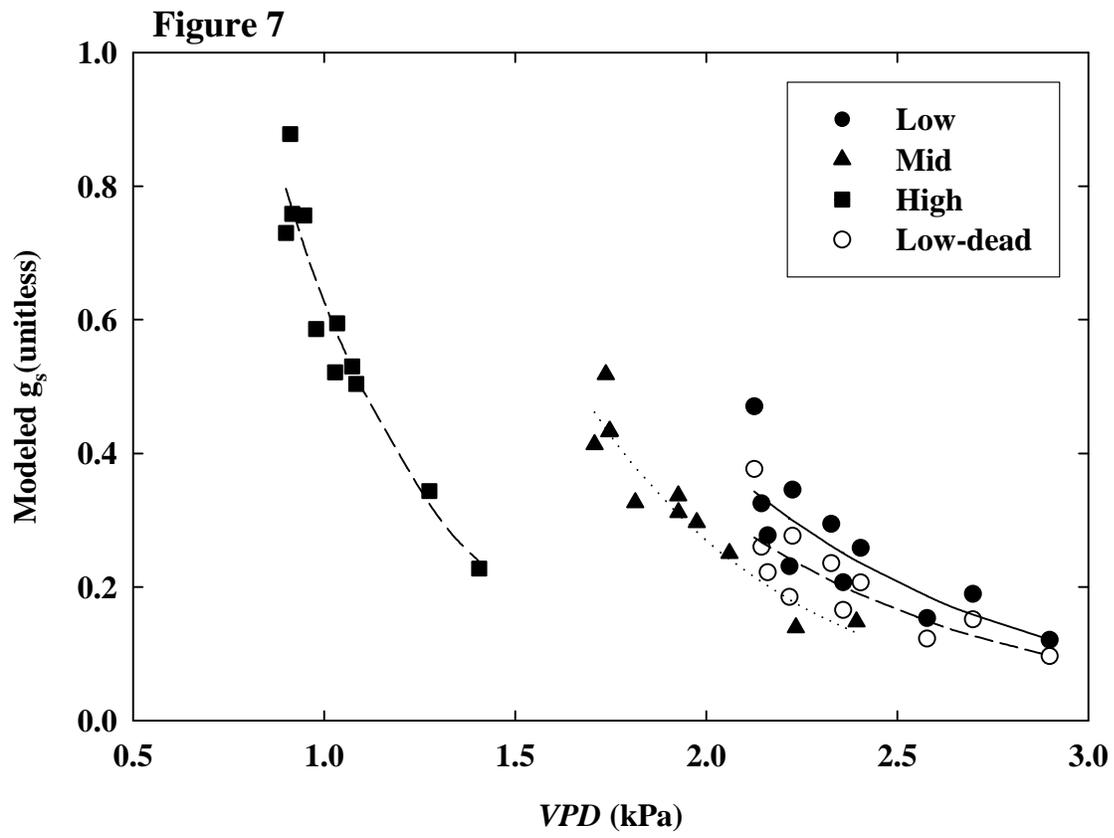
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Figure 6



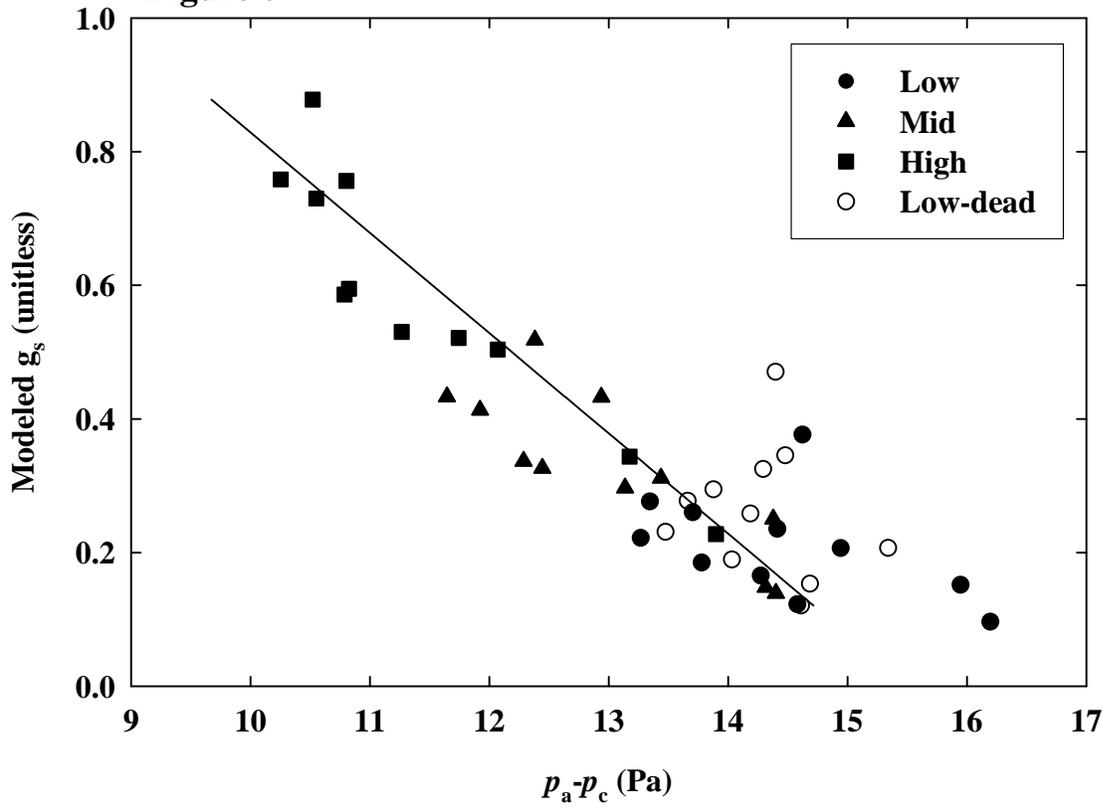
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1



2

Figure 8



1