Climatic limits on foliar growth during major droughts in the southwestern USA

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[1] Pronounced droughts during the 1950s and 2000s in the American Southwest provide an opportunity to compare mesoscale ecosystem responses to anomalously dry conditions before and during the regional warming that started in the late 1970s. This year-round warming has produced fewer cool season freezes, losses in regional snowpack, an 8–10 day advance in spring onset, and hotter summers, all of which should affect vegetation differently across seasons and elevations. Here, we examine indices that represent climatic limits on foliar growth for both drought periods and evaluate these indices for areas that experienced tree mortality during the 2000s drought. Relative to the 1950s drought, warmer conditions during the 2000s drought decreased the occurrence of temperatures too low for foliar growth at lower elevations in winter and higher elevations in summer. Higher vapor pressure deficits (VPDs), largely driven by warmer temperatures in the more recent drought, were more limiting to foliar growth from spring through summer at lower and middle elevations. At many locations where tree mortality occurred during the 2000s drought, low-temperature constraints on foliar growth were extremely unlimiting, whereas VPD constraints were extremely limiting from early spring through late autumn. Our analysis shows that in physiographically complex regions such as the Southwest, seasonality and elevational gradients are important for understanding vegetative responses to warming. It also suggests that continued warming will both increase the degree to which VPD limits foliar growth during future droughts and expand its reach to higher elevations and other seasons.

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1. Introduction

[2] An increase in temperatures since the late 1970s, partly attributed to human-caused climate change and positively reinforced by Pacific climate variability [*Hegerl et al.*, 2007; *Meehl et al.*, 2007; *Barnett et al.*, 2008; *Bonfils et al.*, 2008], has profoundly impacted hydroclimatology and ecosystem dynamics in western North America. Hydroclimatic impacts include higher freezing levels [*Abatzoglou*, 2011], lower ratios of snowfall to total winter precipitation [*Knowles et al.*, 2006], increases of rain-on-snow events [*McCabe et al.*, 2007], and shifts to earlier snowmelt [*Stewart et al.*, 2005] and attendant losses in snowpack [*Mote et al.*, 2005; *McCabe and Wolock*, 2009]. Well-documented ecological impacts consist of fewer cool season freezes [*Weiss and Overpeck*, 2005], earlier flowering and leafout [*Cayan et al.*, 2001; *Bowers*, 2007; *Crimmins et al.*, 2009; *Ault et al.*, 2011], earlier emergence for insects [*Forister and Shapiro*, 2003], advanced breeding for birds [*Brown et al.*, 1999], and increases in large fires [*Westerling et al.*, 2006]. Another potential impact of the ongoing regional warming is alteration of vegetative responses to recent and future droughts, specifically through changes to climatic limits on foliar growth.

[3] Drought can substantially impact vegetation in the southwestern United States (SW), a physiographically complex region that spans warm deserts in the lowlands and cool, wet boreal forests in the highlands. For example, major droughts in the 1950s and 2000s induced considerable plant mortality in desertscrub, grasslands, woodlands, and forests that resulted in ecotone shifts and altered community composition and structure [*Neilson*, 1986; *Allen and Breshears*, 1998; *Swetnam and Betancourt*, 1998; *Breshears et al.*, 2005; *Negrón et al.*, 2009; *McAuliffe and Hamerlynck*, 2010]. Studies link mortality during the 2000s drought in particular to the ability of warmer temperatures to drive

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higher water stress [*Breshears et al.*, 2005; *Adams et al.*, 2009] and intensified insect outbreaks [*Logan et al.*, 2003; *Raffa et al.*, 2008]. Temperatures were above average during both the 1950s and 2000s droughts and considerably warmer during the more recent drought [see *Weiss et al.*, 2009, Figure 1] resulting in higher vapor pressure deficits (VPDs) [*Weiss et al.*, 2009]. A comparison of the 1950s and 2000s droughts thus offers a unique opportunity to investigate mesoscale ecosystem responses such as mortality and foliar growth to two remarkable climatic events.

[4] In addition to drought variability in the SW, recent warming is superimposed on a highly seasonal climate and complex topography. Temperature follows the typical seasonal cycle from a winter minimum to a summer maximum, whereas most of the precipitation occurs at two distinct times of the year [*Sheppard et al.*, 2002]. From winter through early spring, westerly frontal systems deliver both rain and snow, whereas from midsummer through early autumn the North American monsoon (hereafter monsoon) and, to a lesser degree, dissipating tropical cyclones from the eastern Pacific Ocean supply rain. Prominence of either of these peaks in the annual precipitation cycle is spatially variable, with a regional gradient from a cool-season regime in the northwest to one strongly influenced by the monsoon in the southeast. The period from late spring through early summer, often referred to as the foresummer, separates these two relatively wet seasons and is climatologically the hot and dry part of the year. Terrain ranges from elevations below sea level to above treeline [see *Weiss et al.*, 2009, Figure 3] and promotes lower temperatures and greater precipitation at higher elevations due to adiabatic cooling and orographic effects, respectively. The seasonality and environmental gradients in this subtropical region lead to short growing seasons for high-elevation forest and tundra in summer [*Inouye*, 2008], and bimodal growing seasons at lower elevations and latitudes that receive both cool and warm season precipitation [*Weiss et al.*, 2004; *Crimmins et al.*, 2008; *Crimmins et al.*, 2011].

[5] Differences in temperature and moisture between the 1950s and 2000s droughts in the SW may have approached or crossed thresholds of climatic limits on foliar growth, i.e., climatic controls on photosynthesis and transpiration such as low temperature and high VPD, both seasonally and along elevational gradients. As detailed by *Weiss et al.* [2009], the main distinction between these events is that much of the region experienced warmer temperatures that increased VPDs during the foresummer in the 2000s drought. Warmer temperatures and greater VPDs continued into midsummer and early autumn during the 2000s drought, but mainly for parts of the region where monsoon rainfall does not dominate the annual precipitation cycle. Warming and drying can affect vegetation if they approach or cross thresholds at which foliar growth becomes inactive or unconstrained. For example, conditions during the 2003 summer heat wave in the Swiss Alps approached or crossed low-temperature and VPD thresholds at different elevations [*Jolly et al.*, 2005a]. Vegetative growth increased with lengthening of the growing season at higher elevations, but it decreased in moisture-limited environments at lower elevations due to increased water stress.

[6] In our SW case, we anticipated that warmer conditions during the 2000s drought relative to the 1950s drought led to similarly divergent changes in how climate limited foliar growth of regional vegetation. We also hypothesized that due to the Southwest's highly seasonal climate and complex topography, spatiotemporal variability associated with these two droughts additionally changed climatic constraints on foliar growth. In particular, we expected: (1) that greater VPD in the foresummer during the 2000s drought [*Weiss et al.*, 2009] was more limiting to foliar growth at lower elevations than during the 1950s drought; (2) that these more limiting conditions of the 2000s drought also took place outside of the southeast part of the region from midsummer through early autumn; (3) that warmer summers during the more recent drought decreased the occurrence of temperatures too low for foliar growth at higher elevations; and (4) that warmer springs and autumns decreased the occurrence of temperatures too low for foliar growth at lower elevations.

[7] To examine these anticipated effects of drought and a warming climate on vegetation, we compared seasonal values of indices that represent climatic limits on foliar growth based on low temperature and VPD between the 1950s and 2000s droughts, and inspected these differences along elevational gradients for the entire region. We also assessed the extremeness of climatic limits on foliar growth with these indices at locations where tree mortality occurred during the 2000s drought. Our intent was not to compare mortality during these major droughts, but rather to use differences in climatic limits on foliar growth between the two events to show how warmer temperatures already may be impacting vegetation across a physiographically complex region.

2. Data and Methods

2.1. Indices of Climatic Limits on Foliar Growth

[8] We computed indices that represent climatic limits on foliar growth during the 1950s and 2000s droughts using gridded observational data compiled by the PRISM Group at Oregon State University (www.prism.oregonstate.edu). PRISM data are meteorological station data interpolated to 4-km grid cells using a human-expert and statistical knowledge-based system [*Daly et al.*, 2002]. By accounting for physiographic features such as the elevation at and vertical layer in which a grid cell occurs, observations at several meteorological stations of varying proximity to a grid cell, and the topographic orientation of a grid cell, PRISM data show improvement over other gridded climate data products in topographically complex and data-sparse regions [*Daly et al.*, 2008; *Minder et al.*, 2010]. We used PRISM monthly means of maximum temperature (°C), minimum temperature (°C), and dew point temperature (°C). We also calculated monthly means of VPD (kPa), the difference between saturation and actual vapor pressure, using PRISM data and the formula:

$$VPDmean = a\exp\left(\frac{b\ Tmean}{Tmean + c}\right) - a\exp\left(\frac{b\ Tdmean}{Tdmean + c}\right), \quad (1)$$

where a = 0.611 kPa, b = 17.502, c = 240.97°C, *VPDmean* = monthly mean VPD (kPa), *Tmean* = monthly mean temperature (°C), and *Tdmean* = monthly mean dew point temperature (°C) [*Campbell and Norman*, 1998]. Both dew point temperature and VPD are measures of atmospheric moisture, with the latter being an estimate of the atmospheric demand for evapotranspiration (ET). The spatial domain for our study is the region from 27°N to 43°N and 117°W to 100°W [see *Weiss et al.*, 2009, Figure 3], with particular focus on the states of Arizona, Colorado, New Mexico, and Utah. PRISM data were only available for domain areas within the United States, and thus our analysis only included the southwest region of the United States, rather than extending into Mexico.

[9] We used monthly means of minimum temperature and VPD to calculate monthly index values of limits on foliar growth based on low temperature and ET demand, respectively [*Jolly et al.*, 2005b]. We also computed a monthly foliar-growth-limit index based on photoperiod (i.e., day length), which is a function of solar declination and latitude [*Campbell and Norman*, 1998], for the PRISM grid mesh. Known minimum-temperature, VPD, and photoperiod limits on foliar growth define corresponding index values that vary linearly between inactive (i.e., foliar growth is not occurring; value = 0) and unconstrained (i.e., foliar growth is unlimited; value = 1) thresholds [see *Jolly et al.*, 2005b, Figure 1]. The inactive threshold for minimum temperature is −2°C, and the unconstrained is +5°C. For VPD, the inactive threshold is +4.1 kPa and the unconstrained is +0.9 kPa. Photoperiod has inactive and unconstrained thresholds of 10 and 11 h, respectively. Beyond the inactive threshold, index values equal zero, whereas index values equal one beyond the unconstrained threshold.

[10] As these thresholds represent measurements of climatic limits on foliar growth from a global array of species, we felt they were appropriate for our generalized analysis of the spatially variable vegetation in the SW. Inactive and unconstrained thresholds of minimum temperature and photoperiod primarily reflect the phenological states of dormancy and budburst, respectively (S. Running, personal communication). Average photoperiods during the months of November, December, and January fall between 10 and 11 h at many northerly latitudes in the SW, whereas they remain above 11 h at the most southerly latitudes. In contrast, VPDs above the unconstrained threshold value indicate conditions that limit foliar growth through physiological stress in leaves. Although precipitation is another climatic limit on foliar growth, *Jolly et al.* [2005b] did not develop it as one of their foliar growth indices due to its discrete nature and lack of data availability in some parts of the world, and we do not address it in this study.

[11] We also calculated monthly values of a growing season index (iGS), defined as the product of the monthly values of foliar-growth-limit indices based on low temperature (iTmin), ET demand (iVPD), and photoperiod [*Jolly et al.*, 2005b]. Values of the iGS represent a generalized model of climatic constraints on foliar growth that integrates the individual effects of these three limits during the year. *Jolly et al.* [2005b] showed that iGS is a robust proxy of foliar growth variability in space and time for a variety of biotic communities, and is appropriate for historical analyses. By definition, iGS ranges from zero (inactive) to one (unconstrained).

2.2. Comparison of the 1950s and 2000s Droughts

[12] We defined the analysis periods for the 1950s and 2000s droughts as the four-year periods 1953–1956 and 2000–2003, respectively, after *Weiss et al.* [2009]. We used gridded monthly values of iTmin, iVPD, and iGS from December 1952 to January 1957 and from December 1999 to January 2004 to calculate three-month mean seasonal values centered on each calendar month for both drought periods. For example, the seasonal January (i.e., December–January–February) 1953 iTmin value is the average of iTmin monthly values from December 1952, January 1953, and February 1953. Thus, for statistical tests described below, we used a seasonal value for each foliar-growth-limit index and month from January 1953 through December 1956 for the 1950s drought, and from January 2000 through December 2003 for the 2000s drought.

[13] We performed nonparametric Wilcoxon rank sum tests to determine local statistically significant differences (i.e., at individual PRISM grid cells) between seasonal location parameters (analogous to mean values) of the 1950s and 2000s droughts for iTmin, iVPD, and iGS [*Wilks*, 2006]. We regarded values of a particular foliar-growth-limit index and season in a drought period (e.g., the four iTmin values for December–January–February from 1953 to 1956) as temporally independent for sample size calculation. We also evaluated whether or not results from one season were independent from results in other seasons for each index. In general, the e-folding time through the study domain indicates that results from seasons with non-overlapping months can be viewed as independent. To address possible spatial autocorrelation in fields of joint Wilcoxon rank sum tests, we carried out nonparametric field significance tests with a permutation randomization approach of 500 iterations [*Livezey and Chen*, 1983; *Wilks*, 2006]. We conducted all tests at the 95% level.

2.3. Extremeness of Climatic Limits at Mortality Locations

[14] To characterize the extremeness of climatic limits on foliar growth during the 2000s drought, we calculated percentile values of seasonal iTmin, iVPD, and iGS on a cell-by-cell basis for all four-year seasonal medians from 1895 through 2003. From the percentile data, we selected PRISM grid cells that intersect with locations where tree mortality occurred in SW woodlands and forests during the 2000s drought. Similar mortality data of the 1950s drought were not available, so we limited our evaluation to sites that experienced mortality during the more recent drought. Geographic information system shapefiles produced by DIREnet (www4.nau.edu/direnet/index.html) delineate these locations and represent a suitable regional sample of tree mortality during the 2000s drought. DIREnet creates regional mortality shapefiles by tree species through use of U.S. Forest Service (Intermountain, Rocky Mountain, and Southwest regions) aerial survey data of tree mortality. These aerial surveys annually map trees undergoing foliage discoloration and defoliation from biotic and abiotic agents while disregarding those that appear to have died in previous years. We utilized annual mortality shapefiles from 2000 through 2003 for *Abies concolor* (white fir), *A. lasiocarpa* (subalpine fir), *Picea spp.* (spruce), *Pinus edulis* and *P. monophylla* (pinyon

pine), *P. flexilis* (limberpine), *P. ponderosa* (ponderosa pine), and *Pseudotsuga menziesii* (Douglas-fir). We accessed these mortality data in August 2010. For the purpose of this study, we merged mortality shapefiles of individual years and species to create one mortality shapefile for the four-year period 2000–2003 and for all of the above species.

3. Results

[15] We first present the results from seasonal Wilcoxon rank sum and field significance tests in map form for foliar-growth-limit indices based on low-temperature (iTmin), ET-demand (iVPD), and integrated-growing-season (iGS) limits. We display maps for results of all seasons in order to show how differences in climatic limits on foliar growth between the 1950s and 2000s droughts vary across the region and change at different times of the year. However, we only describe locally significant results for seasons that are field significant. We also present these results as scatterplots of significant seasonal differences versus elevation. We then show the extremeness of seasonal climatic limits on foliar growth at locations where tree mortality occurred in SW woodlands and forests during the 2000s drought in bar graph form.

3.1. Wilcoxon Rank Sum and Field Significance Tests

3.1.1. iTmin

[16] Seasonal iTmin during the 1950s and 2000s droughts in the SW shows differences that are field significant only in midwinter and from midspring through midautumn (Figure 1). Locally significant positive differences occur in various areas throughout the region in December–January–February and from March–April–May through September–October–November. Values mostly range from +0.10 to +0.40, indicating that low temperatures in these seasons were less limiting to foliar growth during the 2000s drought than the 1950s drought. Locally significant negative differences are few during these seasons. The predominantly positive locally significant differences in the region move from lower elevations in midwinter to higher elevations in midsummer and back again (Figure 2).

3.1.2. iVPD

[17] Seasonal iVPD for the 1950s and 2000s droughts shows field significant differences only from midspring through late summer, and indicates that VPDs were more limiting to foliar growth during the more recent drought at these times of the year (Figure 3). In March–April–May and April–May–June, locally significant negative differences are widespread in southern New Mexico, Arizona, southern Utah, and the western periphery of the region. Locally significant and widespread negative differences decline in southern New Mexico and southeastern Arizona, expand into northern Utah, and appear in western Colorado from May–June–July through July–August–September. Values generally range from −0.05 to −0.30. Locally significant positive differences are few during these seasons. In the midspring through late summer period, the mostly negative locally significant differences occur mainly at lower elevations, and extend into middle elevations during summer (Figure 2).

3.1.3. iGS

[18] Field significant differences of seasonal iGS between the 1950s and 2000s droughts appear only in midwinter and from midspring through late autumn (Figure 4). In December–January–February and from March–April–May through October–November–December, locally significant positive differences occur in various areas throughout the region and largely correspond to iTmin results (Figure 1). Values mostly range from +0.10 to +0.40 and indicate that integrated climatic limits in these areas and seasons were less constraining to foliar growth during the more recent drought (Figure 4). In contrast, locally significant negative differences from March–April–May through July–August–September that in general correspond to iVPD results (Figure 3) mainly occur in the southern and western parts of the region, and are especially widespread in Arizona from April–May–June through July–August–September and in Utah during June–July–August and July–August–September (Figure 4). Values mostly range from −0.05 to −0.30 and show that integrated climatic limits in these areas and seasons were more constraining to foliar growth during the more recent drought. Locally significant negative differences are few in December–January–February and from August–September–October through October–November–December. To a great extent, the elevational profiles of locally significant seasonal iGS differences follow a combination of those of iTmin and iVPD (Figure 2). Locally significant positive differences largely move from lower elevations in midwinter to higher elevations in midsummer and back again, whereas locally significant negative differences mainly occur at lower and middle elevations from midspring through late summer. A transition from locally significant negative to locally significant positive differences is evident at middle elevations from late spring through late summer.

3.2. Extremeness of Climatic Limits at Mortality Locations

[19] We present the extremeness of seasonal climatic limits on foliar growth at locations where tree mortality occurred in SW woodlands and forests during the 2000s drought in bar graph form (Figure 5). Each seasonal panel contains information about a foliar-growth-limit index for the 2000s drought organized along percent and elevation axes. Successive 500-m ranges comprise the elevation axis. For each 500-m elevational range, we show two bars. One depicts the percent of PRISM grid cells that intersect tree mortality locations within that elevational range whose foliar-growth-limit index values are above the 95th percentile. The other represents the percent of such cells within that elevational range whose values are below the 5th percentile. Of the 12,685 PRISM grid cells that intersect with mortality locations, almost all occur between elevations of 1500 and 3500 m (Table 1).

[20] For example, 100% of the PRISM grid cells that intersect tree mortality locations between 500 and 1000 m in elevation have iGS values that are below the 5th percentile during June–July–August of the 2000s drought (Figure 5). Values for iGS are also below the 5th percentile for the majority of cells within the 1000–1500, 1500–2000, and 2000–2500 m elevational ranges. Very few to no cells within these elevational ranges have values above the 95th percentile. Between 2500 and 3000 m, however, 14% of cells have values below the 5th percentile, whereas 20% of cells have values above the 95th percentile. In further contrast, the majority of cells in the 3000–3500 and 3500–4000 m elevational ranges have values above the 95th percentile. Less than

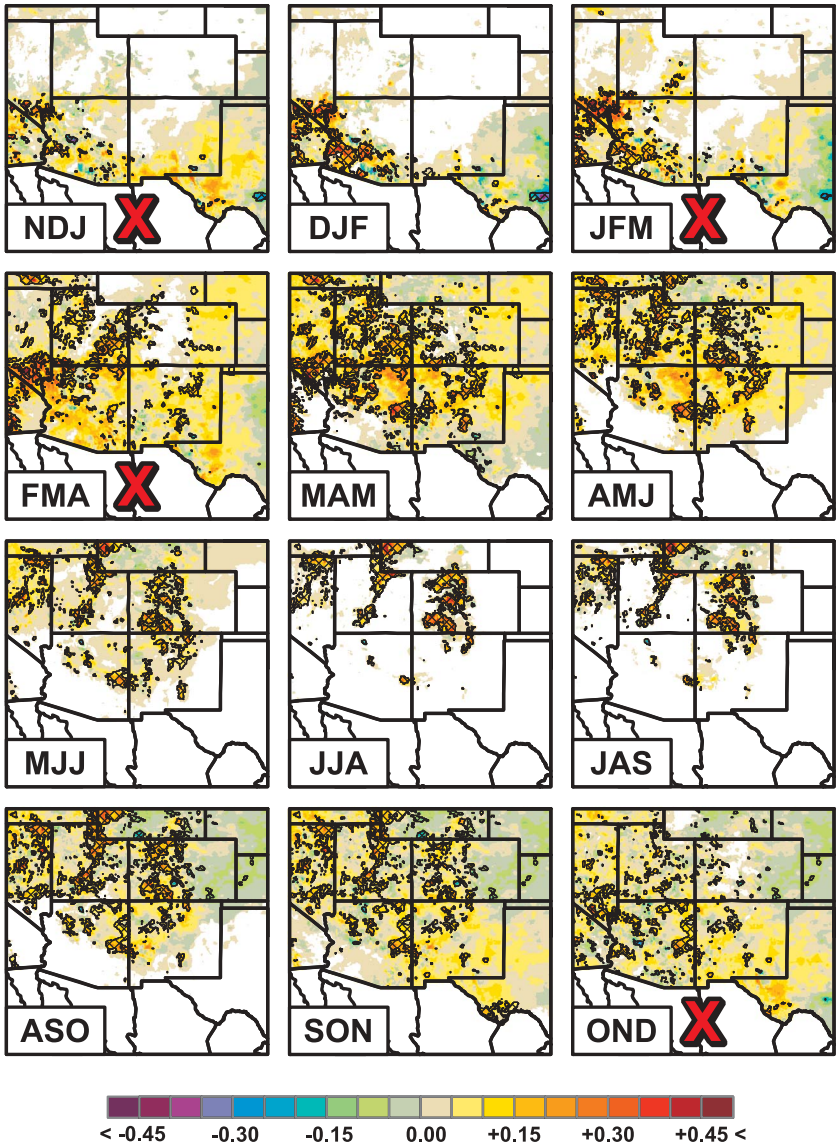

Figure 1. Wilcoxon rank sum and field significance test results for seasonal iTmin. Color gradation quantifies unitless differences between seasonal median values of the 2000s and 1950s droughts (e.g., December–January–February iTmin median$_{2000–2003}$ − December–January–February iTmin median$_{1953–1956}$). The first letter of each month in a given season comprises the abbreviated seasonal name for each map (e.g., DJF for December–January–February). White areas in the United States denote locations with index values of zero (inactive) or one (unconstrained) for both drought periods. Cross-hatched areas are locally significant at the 95% level. Seasonal maps with a red X are not field significant at the 95% level. Positive (negative) values indicate that low temperatures were less (more) limiting to foliar growth during the 2000s drought than the 1950s drought.

3% of cells in each of these upper elevational ranges have values below the 5th percentile. Overall, these percentages indicate that integrated climatic constraints were extremely limiting to foliar growth during midsummer of the 2000s drought below 2500 m in elevation at most mortality locations. Above 3000 m, these constraints were extremely unlimiting for a majority of these locations. Again, bar graphs do not depict mortality locations of the 1950s drought.

3.2.1. iTmin

[21] Many seasonal iTmin values of the 2000s drought at locations of tree mortality are above the 95th percentile, indicating that low-temperature constraints were extremely unlimiting to foliar growth during this time period in several of these areas (Figure 6). These relatively extreme high values mainly occur from early spring through late autumn and vary in elevation depending on the season, similar to the seasonal variability in elevation of locally significant iTmin differences between the two droughts (Figure 2). No more than 19% of cells that intersect tree mortality locations have iTmin values above the 95th percentile in elevational ranges below 3000 m from November–December–January through January–February–March of the 2000s drought (Figure 6).

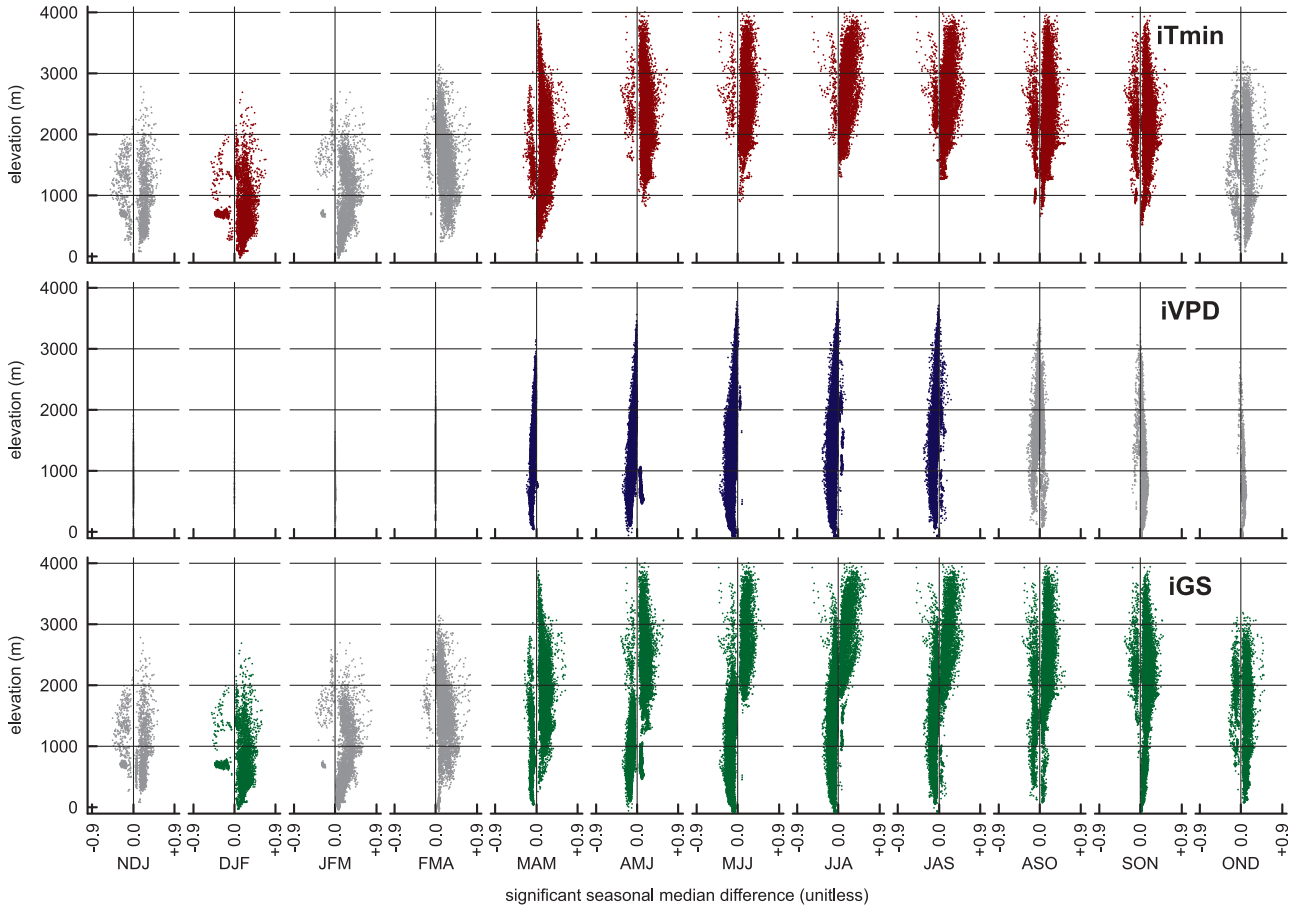

Figure 2. Scatterplots of locally significant differences between seasonal median values of the 2000s and 1950s droughts and corresponding elevations for iTmin (red), iVPD (blue), and iGS (green). The first letter of each month in a given season comprises the abbreviated seasonal name for each scatterplot (e.g., DJF for December–January–February). Positive (negative) values indicate that the 2000s drought was less (more) limiting than the 1950s drought to foliar growth. Scatterplots in gray represent seasonal maps that are not field significant at the 95% level (Figures 1, 3, and 4).

Above 3000 m, no cells have such values. Between 18% and 53% of cells with values above the 95th percentile are in elevational ranges from 1000 to 3000 m during February–March–April. The percent of cells with values greater than the 95th percentile increases for upper elevational ranges in March–April–May and April–May–June, with these relatively extreme high values appearing at a majority of cells in almost all ranges above 1500 m. From May–June–July through July–August–September, the percent of cells with values above the 95th percentile declines at lower elevational ranges while continuing to account for a majority of cells in ranges above 3000 m. The number of cells with values above the 95th percentile increases during August–September–October, September–October–November, and October–November–December at most lower elevational ranges, comprising between 20% and 50% of the total in many cases. The percent of cells with these relatively extreme high values declines at elevational ranges above 3000 m during these seasons. Seasonal iTmin values below the 5th percentile occur much less frequently throughout the year, and total no more than 4% of cells within any elevational range and season.

3.2.2. iVPD

[22] In contrast to iTmin, many seasonal iVPD values at mortality locations during the 2000s drought are below the 5th percentile, suggesting that constraints of VPDs were extremely limiting to foliar growth during this time interval in many of these areas (Figure 7). These relatively extreme low values appear mostly from early spring through late autumn and vary in elevation depending on the season, similar to the seasonal variability in elevation of locally significant iVPD differences between the two droughts (Figure 2). Less than 1% of cells that intersect tree mortality locations in any elevational range have iVPD values below the 5th percentile from November–December–January through January–February–March during the 2000s drought (Figure 7). In February–March–April, cells with values below the 5th percentile are between 1% and 49% of the total in elevational ranges from 1000 to 3000 m. Relatively extreme low values account for a higher percent of cells in each of these elevational ranges during March–April–May, and appear in all elevational ranges during April–May–June. Values below the 5th percentile occur at a large majority of cells in lower elevational ranges during these two seasons. From May–June–July through July–August–September, all

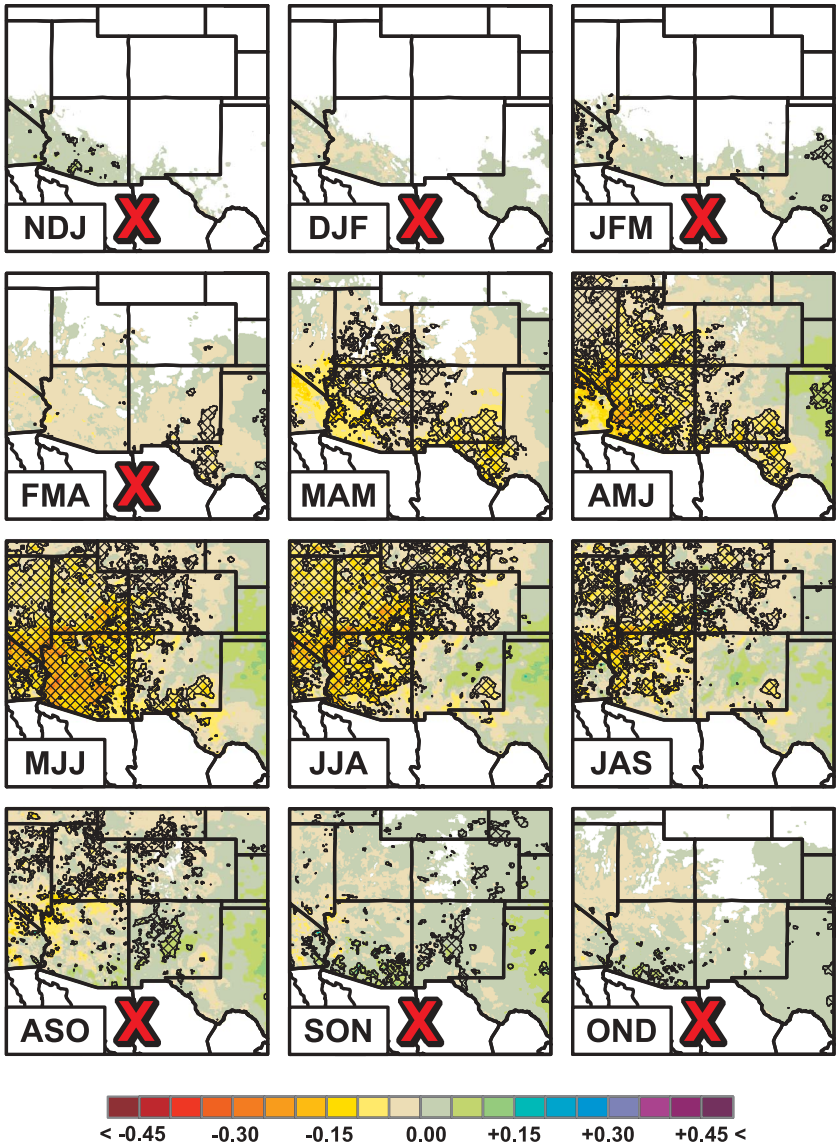

Figure 3. As in Figure 1, but for iVPD. Positive (negative) values indicate that VPDs were less (more) limiting to foliar growth during the 2000s drought than the 1950s drought.

elevational ranges have a large majority of cells with values below the 5th percentile. Cells with these relatively extreme low values are not as numerous as in these seasons for any elevational range in August–September–October, most notably at upper ranges. Nonetheless, between 50% and 60% of cells have relatively extreme low values in elevational ranges from 500 to 2500 m at this time of year. The number of cells with values below the 5th percentile decreases further in September–October–November and October–November–December, comprising between 0% and 43% of the total in the elevational ranges. Seasonal iVPD values above the 95th percentile comprise less than 1% of cells within any elevational range and season.

3.2.3. iGS

[23] Seasonal iGS values above the 95th percentile or below the 5th percentile occur at many locations of tree mortality during the 2000s drought, showing that integrated climatic constraints were extremely unlimiting or limiting, respectively, to foliar growth in several of these areas from 2000 through 2003 (Figure 8). The relatively extreme values mainly appear from early spring through late autumn and vary seasonally in elevation, similar to the seasonal variability in elevation of locally significant iGS differences between the two droughts (Figure 2). Less than 19% of cells that intersect tree mortality locations have iGS values above the 95th percentile in elevational ranges below 3000 m from November–December–January through January–February–March of the 2000s drought (Figure 8). No cells have such values above 3000 m. Also during these seasons, less than 1% of cells in any elevational range have values below the 5th percentile. In February–March–April, cells with values above the 95th percentile are between 18% and 50% of the total in elevational ranges from 1000 to 3000 m, whereas cells with values below the 5th percentile comprise less than 1% in any of these elevational ranges. Relatively extreme high values account for a greater percent of cells for upper

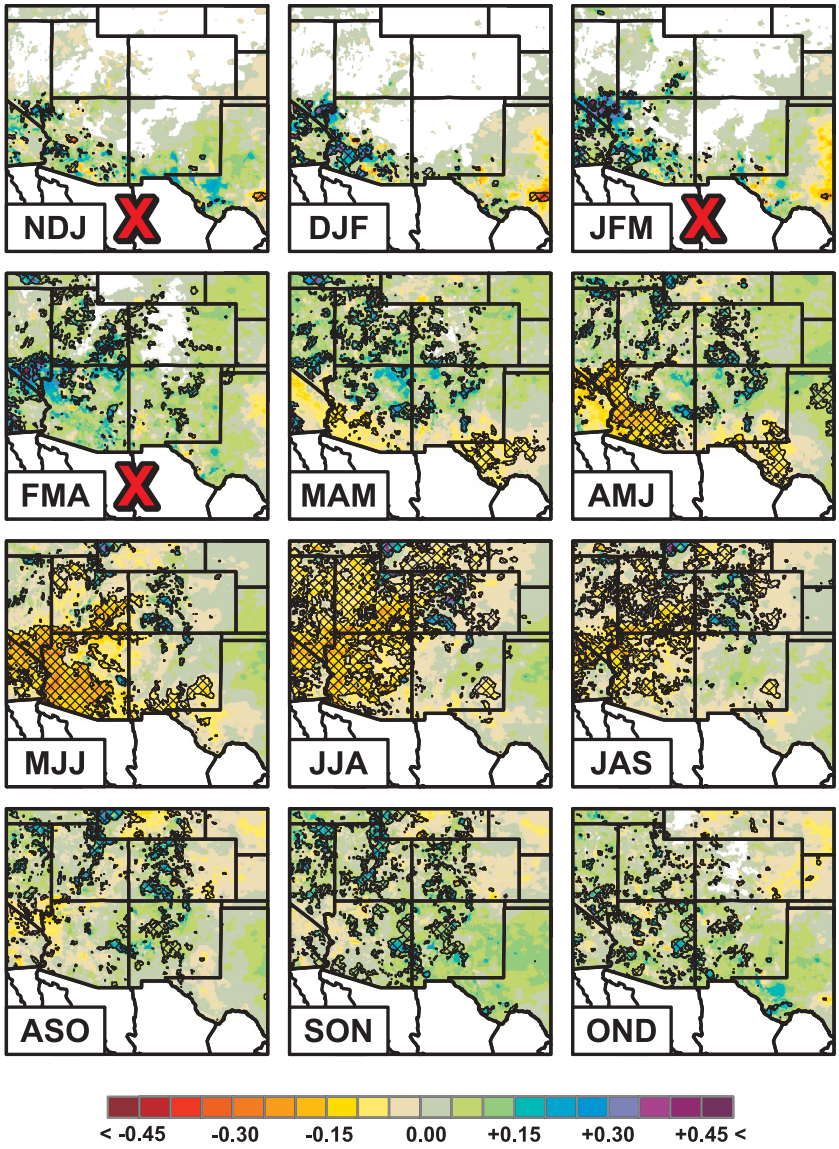

Figure 4. As in Figure 1, but for iGS. Positive (negative) values indicate that integrated climatic constraints were less (more) limiting to foliar growth during the 2000s drought than the 1950s drought.

elevational ranges in March–April–May and April–May–June. In contrast, lower elevational ranges show increasing percentages of relatively extreme low values during these seasons. From May–June–July through July–August–September, the amount of cells with values above the 95th percentile remains large in the 3000–3500 and 3500–4000 m elevational ranges, with percentages between 49% and 90%. The number of cells with values below the 5th percentile during these seasons is considerable at elevational ranges below 2000 m, where percentages vary from 48% to 100%. In elevational ranges above 2000 m, these relatively extreme low values appear in 1% to 55% of cells. The number of cells with values above the 95th percentile comprises 7% to 67% of elevational ranges above 1000 m in August–September–October, September–October–November, and October–November–December. These percentages decrease at upper elevational ranges as this time of year advances, whereas they increase at most lower elevational ranges. Between 1% and 53% of cells with relatively extreme low values occur in August–September–October, with larger percentages at lower elevational ranges. Seasonal iGS values below the 5th percentile appear infrequently during September–October–November and October–November–December, and total no more than 6% of cells within any elevational range.

4. Discussion

[24] Warmer temperatures in the SW appear to be shifting climatic limits on foliar growth in a complicated, yet understandable, way. In our comparison of the 1950s and 2000s droughts, examination of these limits both seasonally and along elevational gradients is important for this understanding. Minimum temperatures near the range from −2°C to +5°C strongly conform in space to the intricate regional terrain, and move from low elevations in winter to the highest elevations in summer and back again (Figure 9). As

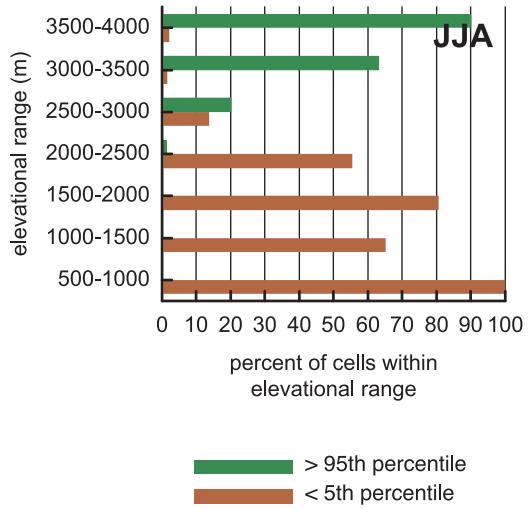

Figure 5. Bar graph characterizing the extremeness of iGS values during June–July–August (JJA) at locations of woodland and forest tree mortality during the 2000s drought. For each 500-m elevational range (i.e., $500 < x \leq 1000$, $1000 < x \leq 1500$, …), bars depict the percent of PRISM grid cells that intersect tree mortality locations where iGS values are above the 95th percentile or below the 5th percentile within that range. Values above the 95th percentile (green) indicate that integrated climatic constraints were extremely unlimiting to foliar growth, whereas values below the 5th percentile (brown) suggest that these constraints were extremely limiting. This bar graph does not depict mortality locations of the 1950s drought.

a result, warmer minimum temperatures that are widespread throughout the region in many seasons during the more recent drought [*Weiss et al.*, 2009] are spatially and temporally restricted in changing constraints of low temperatures on foliar growth. Despite this restriction, warmer minimum temperatures during the 2000s drought decreased the occurrence of temperatures too low for foliar growth from low-elevation subtropical desert in midwinter [*Weiss and Overpeck*, 2005] to high-elevation forest and tundra in the summer [*Inouye*, 2008].

[25] Warmer temperatures that drove higher VPDs during the 2000s drought for much of the SW from midspring through late summer [*Weiss et al.*, 2009] also have a spatially and temporally restricted effect on the constraints that VPD places on foliar growth. VPDs near the range from +0.9 kPa to +4.1 kPa distinctly follow the varied terrain of the region as well, but occur at only the lowest elevations in winter and cover all but the highest elevations in summer (Figure 9). Consequently, constraints of VPD on foliar growth are higher from spring through summer of the 2000s drought, most notably for scrublands, grasslands, and relatively xeric woodlands and forests [*Brown*, 1994]. For differences between the two droughts, the transition between climatic limits of low temperature and VPD is most noticeable during summer at elevations from 2000 to 3000 m (Figure 2). Integration of both low-temperature and VPD constraints throughout the year shows that warmer temperatures affected foliar growth constraints along the entire elevational gradient of the region during the more recent drought.

[26] At many locations of tree mortality in SW woodlands and forests during the 2000s drought, warmer temperatures also appear to push climatic constraints on foliar growth toward relatively extreme levels from early spring through late autumn. As with seasonal differences between the two droughts, relatively extreme values of foliar-growth-limit indices reflect the strong seasonal and elevational connections described above. They also show a pronounced transition during summer from extremely limiting VPDs at lower elevations to extremely unlimiting low temperatures at higher elevations. Interestingly, VPDs during summer of the 2000s drought also limit foliar growth at relatively extreme levels for many mortality locations at higher elevations (Figure 7). However, the influence of VPD on constraining foliar growth in these settings is not as large as that of low temperatures, which continues to dominate the integrated climatic limits on foliar growth (Figure 8). Nonetheless, as temperature-driven water stress and mortality have likely increased throughout elevational ranges of forests in western North America [*van Mantgem et al.*, 2009], physically based process modeling [e.g., *Tague and Band*, 2004] is warranted to determine the influence of relatively extreme VPD at all mortality locations.

[27] The spatial and temporal scales of the PRISM data set used in this study are adequate for regional-scale, generalized analysis of foliar growth limits during the 1950s and 2000s droughts in the SW, as well as for understanding how these limits vary along the elevational gradient throughout the year. Nonetheless, we recognize that there are limitations of PRISM data resolution that may affect our results and their interpretation. Several climatically important terrain and surface features such as elevation, aspect, and land cover vary at spatial scales finer than the 4-km resolution of the PRISM data [*Daly*, 2006]. Variability of elevation within a PRISM grid cell, for example, could produce climatic phenomena such as local cold air drainage or sheltering [*Barry*, 2008], and result in fine-scale variability of low temperatures and VPD that we cannot discern in this study. Similarly, monthly climate data can obscure sub-monthly variations of low temperatures and VPD that affect foliar growth, such as the start and end of the growing season and water stress from hot and dry conditions that are severe over a short length of time. Not fully resolving such sub-monthly events may result in monthly average values of foliar growth indices different from those calculated with daily data. For application of foliar growth indices at different spatial and

Table 1. Number of PRISM Grid Cells That Intersect With Locations Where Tree Mortality Occurred in SW Woodlands and Forests During the 2000s Drought by 500-m Elevational Ranges[a]

Elevational Range	PRISM Grid Cell Count
$3500 < x \leq 4000$ m	141
$3000 < x \leq 3500$ m	1230
$2500 < x \leq 3000$ m	3543
$2000 < x \leq 2500$ m	5041
$1500 < x \leq 2000$ m	2472
$1000 < x \leq 1500$ m	241
$500 < x \leq 1000$ m	17

[a]PRISM grid cell sum = 12,685; x is the elevation of an individual PRISM grid cell.

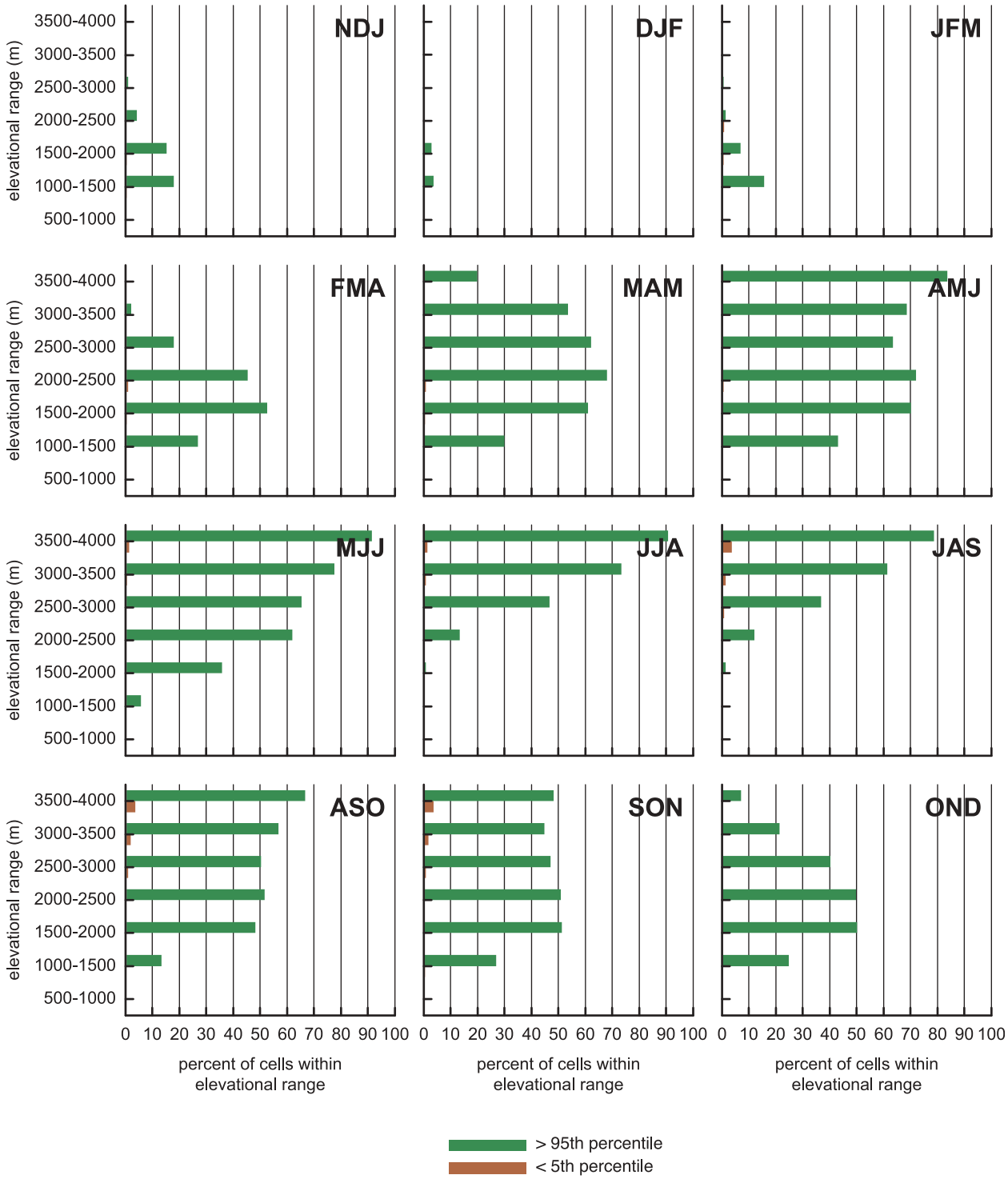

Figure 6. As in Figure 5, but for iTmin values in all seasons. The first letter of each month in a given season comprises the abbreviated seasonal name for each bar graph (e.g., DJF for December–January–February). Values above the 95th percentile (green) indicate that low-temperature constraints were extremely unlimiting to foliar growth, whereas values below the 5th percentile (brown) suggest that these constraints were extremely limiting. Bar graphs do not depict mortality locations of the 1950s drought.

temporal resolutions, scale issues such as these need to be acknowledged.

[28] The importance of elevation in determining seasonal climatic limits on foliar growth highlights the role that spatial variability of climate plays in impacting vegetation during SW droughts. During the 1950s drought, the epicenter of anomalously dry conditions was in the southeastern part of the region, encompassing the U.S.–Mexico

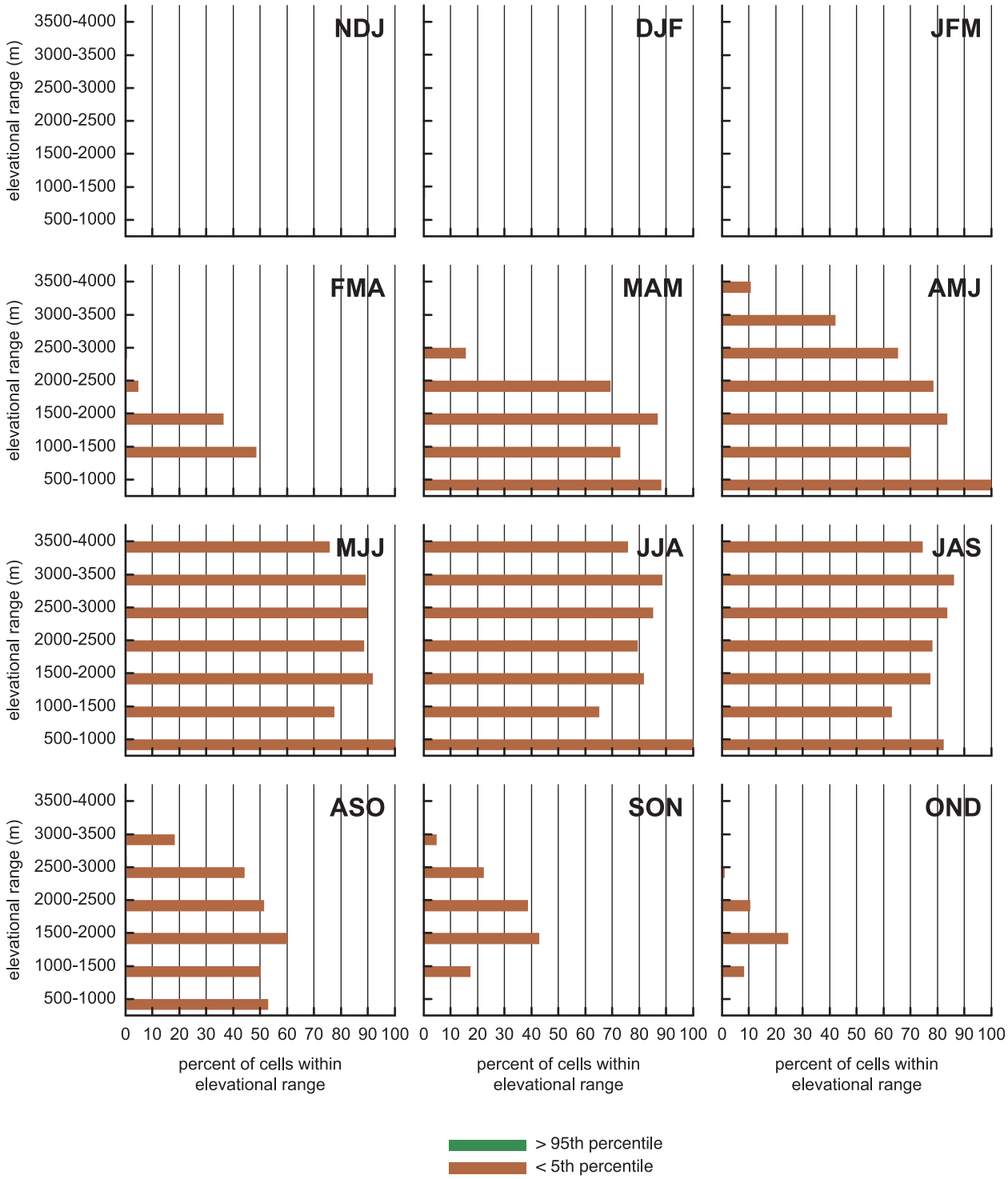

Figure 7. As in Figure 6, but for iVPD. Values above the 95th percentile (green) indicate that constraints of VPD were extremely unlimiting to foliar growth, whereas values below the 5th percentile (brown) suggest that these constraints were extremely limiting.

borderlands and southern High Plains, whereas the epicenter of the 2000s drought was more regionally centered over the Colorado Plateau. Physiography and vegetation shift dramatically from extensive lowlands dominated by desertscrub and grassland in the south to expansive highlands clad in woodlands and forests to the north, across a gain of ~1500 m in elevation [see *Weiss et al.*, 2009, Figure 3]. The different spatial patterns of climatic conditions during the 1950s and 2000s drought likely interacted with regional landscapes to produce dissimilar patterns in ecosystem responses, affecting which species and populations were impacted. For instance, tree mortality in the 1950s drought was most severe in the

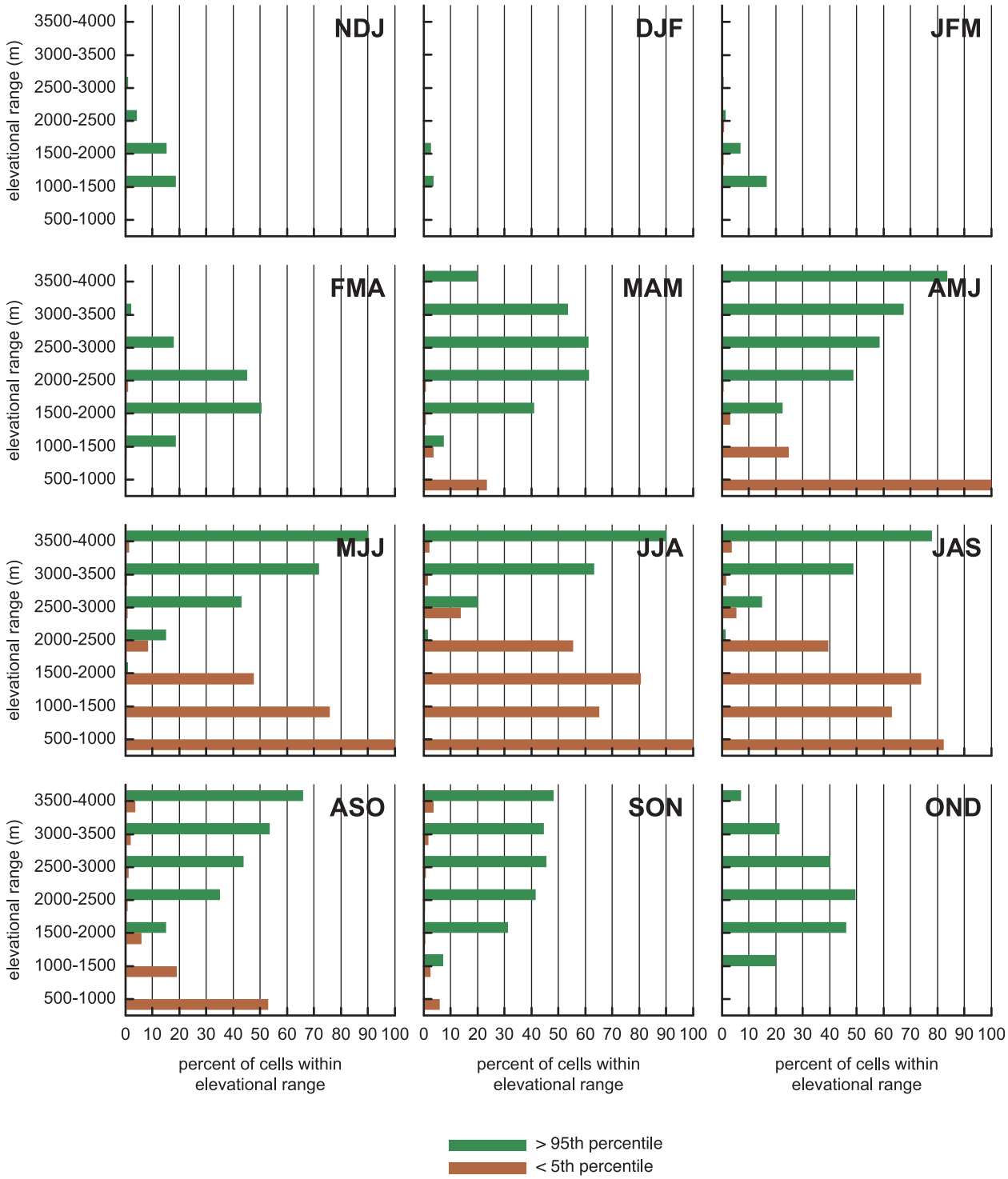

Figure 8. As in Figure 6, but for iGS. Values above the 95th percentile (green) indicate that integrated climatic constraints were extremely unlimiting to foliar growth, whereas values below the 5th percentile (brown) suggest that these constraints were extremely limiting.

south [*Swetnam and Betancourt*, 1998], whereas during the 2000s drought, it was more extensive to the north [*Breshears et al.*, 2005]. In our study, more limiting VPDs from spring through summer during the 2000s drought impacted middle and high elevations to the north (Figure 3), which are commonly occupied by stands of *Pinus edulis* (pinyon pine) and *P. ponderosa* (ponderosa pine). Future studies comparing mesoscale ecosystem responses to the major droughts of the 1950s and 2000s should consider both recent, region-wide warming and intraregional moisture differences, and their interaction with the complex SW physiography.

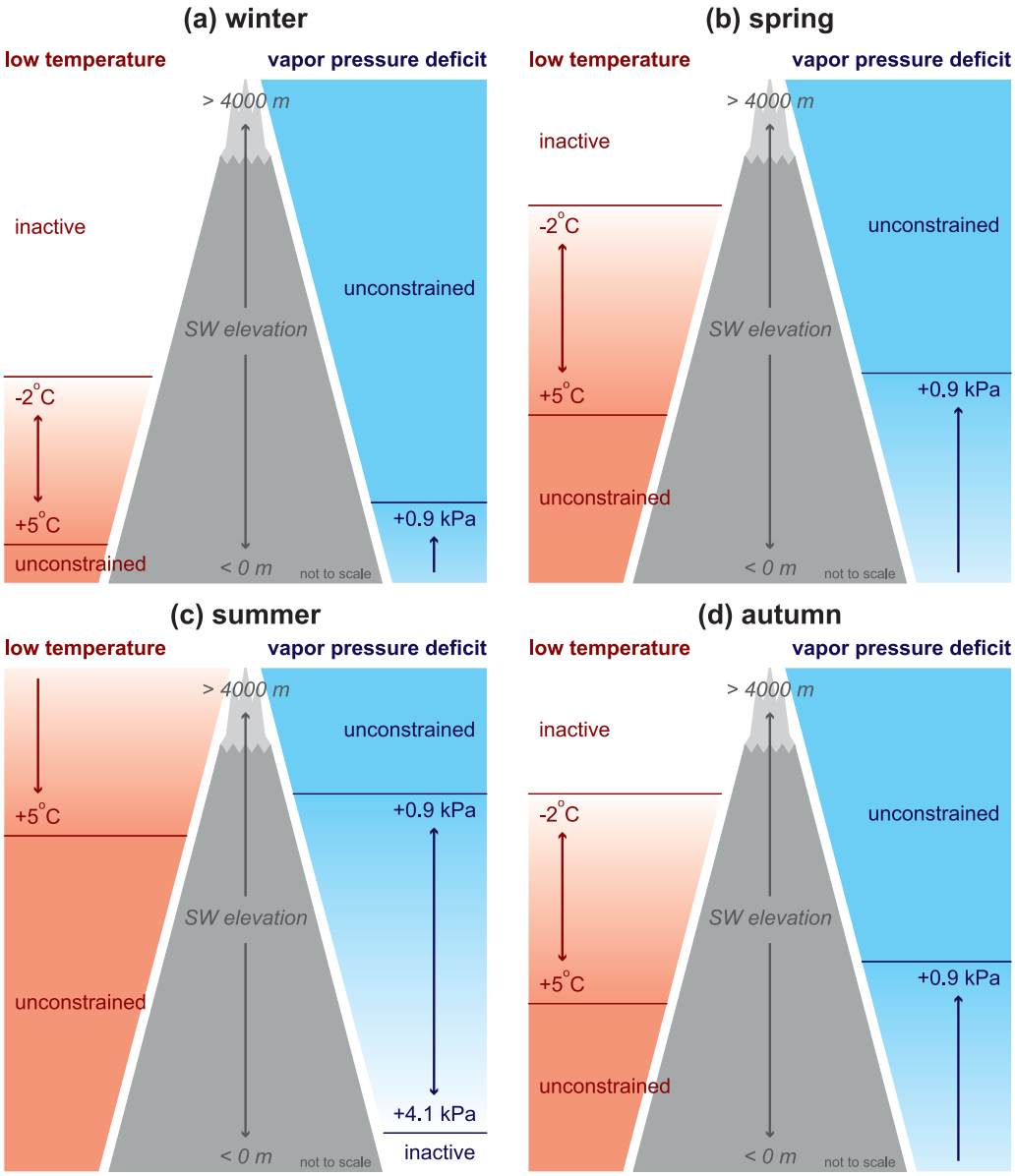

Figure 9. Conceptualization of how low-temperature and VPD limits on foliar growth vary along the elevational gradient of the SW for (a) winter, (b) spring, (c) summer, and (d) autumn. The low-temperature limit has inactive and unconstrained thresholds at minimum temperatures of −2°C and +5°C, respectively. For the VPD limit, the inactive threshold is +4.1 kPa and the unconstrained +0.9 kPa. Both low temperature and VPD have a spatially and temporally restricted influence on the constraints that they individually place on foliar growth. Warmer temperatures during the 2000s drought affected foliar growth constraints along the entire elevational gradient with less limiting low temperatures and more limiting VPD over large parts of the region.

[29] Our analysis suggests that further warming [*Christensen et al.*, 2007; *Karl et al.*, 2009] and episodic drought in the SW during this century will continue to produce climatic conditions that approach or cross thresholds at which foliar growth varies between inactive and unconstrained throughout the elevational gradient. And, at least for locations of tree mortality during the 2000s drought, future climatic constraints on foliar growth under such circumstances will be relatively extreme. Thresholds based on low temperature and VPD will shift to progressively higher elevations for a given season, or similarly occur earlier (later) at the start (end) of the growing season for a given location. Consequently, low-temperature constraints on foliar growth will occur less in space and time, whereas the area over, length of time during, and level to which VPD limits foliar growth will increase. The second outcome is of particular concern as regional warming already is a likely contributor to water stress and tree mortality [*Breshears et al.*, 2005; *van Mantgem et al.*, 2009], and is projected to become increasingly so [*Adams et al.*, 2009; *Williams et al.*,

2010]. Under current rates of global greenhouse gas emissions, higher temperatures in the SW that influence future droughts by potentially raising VPDs are virtually assured [*Christensen et al.*, 2007; *Karl et al.*, 2009]. Amelioration of higher VPDs by monsoon moisture for parts of the region is uncertain, as simulations of monsoon variability are inconsistent [*Liang et al.*, 2008]. Increases in VPD during future regional droughts will not only intensify its constraints on foliar growth where and when it already occurs, but also expand its reach to higher elevations and other seasons.

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