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Plasticity in physiological traits in conifers: Implications for response to climate change in the western U.S.

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Variability in ecophysiological attributes of western U.S. conifers suggests relative capacity of species and populations to respond to environmental change.

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ABSTRACT

Population variation in ecophysiological traits of four co-occurring montane conifers was measured on a large latitudinal gradient to quantitatively assess their potential for response to environmental change. White fir (*Abies concolor*) had the highest variability, gross photosynthetic rate (Pg), and foliar carbon (C) and nitrogen (N) content. Despite low water use efficiency (WUE), stomatal conductance (gs) of fir was the most responsive to unfavorable environmental conditions. *Pinus lambertiana* exhibited the least variability in Pg and WUE, and is likely to be the most vulnerable to environmental changes. *Pinus ponderosa* had an intermediate level of variability, and high needle growth at its higher elevational limits. *Pinus Jeffreyi* also had intermediate variability, but high needle growth at its southern latitudinal and lower elevational limits. The attributes used to assess tree vigor were effective in predicting population vulnerability to abiotic (drought) and biotic (herbivore) stresses.

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1. Introduction

One of the strongest abiotic stressors in western U.S. ecosystems is drought. Drought stress is a common, but not continuous, stress. For example, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) is likely to have experienced severe drought stress approximately one third of the growing seasons in a 125 yr record of precipitation in southern Californian mountains (Grulke et al., 2009). Drought stress occurs seasonally, interannually, as well as over longer terms. This syncopated stress on several different time scales is likely to result in the maintenance of phenotypic plasticity, rather than a fixed adaptation (Agrawal, 2001), especially in long-lived species. Because significant, rapid environmental changes (e.g., drought, excessive O_3 exposure, N deposition, increasing temperature, growing season length) associated with environmental change are likely to occur within the life time of trees, the species will likely persist only if sufficient variation already occurs in the population in a given location. Herbivory, such as imposed by bark beetles, is a strong biotic stressor. In this paper, their presence was used as an indicator of plant stress, as trees of low vigor can be targets for beetle attack (Smith, 1971). Severe drought stress and successful bark beetle attacks are effective agents of change in 'resetting' species distributions (Grulke et al., 2009).

The degree of plasticity is classically determined in common garden experiments with tree seedlings or saplings. This type of experiment tests the interaction between genetic variability and its expression as modified by environmental stresses (Reich et al., 1996). Alternatively, plasticity can also be evaluated for different populations using 'physiological challenges' (*sensu* Valladares et al., 2005). In this paper, measures of ecophysiological attributes of trees relating to carbon, water, and nutrient balance were used to assess the range of combined phenotypic and genotypic variation present in populations along a large latitudinal gradient imposing physiological challenges. For two of the species, sufficient ecological breadth existed to also describe population responses along both elevational and latitudinal gradients.

The latitudinal gradient imposed a range of environmental conditions such as the levels of drought stress experienced (via evapotranspiration and soil water deficits), and their capacity for carbon acquisition and retention (range in temperature and growing season length). The physiological traits chosen were those critical to total carbon budget (gross photosynthesis[1] (Pg), respiration (Rs), and foliar C), water handling capacity (water use efficiency (WUE) and needle elongation growth), and nutrient resources (foliar N), and

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[1] Net assimilation plus foliar respiratory losses during the day.

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represent quantitative measures of tree vigor. The conifers chosen for study were common components of the mixed conifer forest zone (*sensu* Barbour et al., 2007) along a latitudinal gradient from their southern distribution in the Peninsular Range in Baja Mexico through the Transverse Range of southern California, through the Sierra Nevada, to their northern distribution in the southern Cascade Range. Of those investigated, ponderosa pine (*P. ponderosa*) and Jeffrey pine (*Pinus Jeffreyi* Grev. & Balf.) were the most shade intolerant. White fir (*Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr.) and sugar pine (*Pinus lambertiana* Dougl.) were more shade tolerant (Burns and Honkala, 1990). Where species had more ecological breadth, attributes along elevational gradients were also characterized.

In long-lived species such as trees, the variability in extant populations is the 'bag of tricks' available for future environmental conditions over the next several hundred years. Relative to each other, was a similar level of variability present in a given physiological trait among these co-occurring species? Was there evidence of narrowing of or increase in variability at one end of its elevational or latitudinal distribution that suggested relative future failure or success of the population? Were any of the physiological traits associated with susceptibility to herbivore activity (leaf and bole tissue) that would likely lead to increased mortality? For *P. Jeffreyi* and *P. ponderosa*, more data was available including elevational gradients within sites, manipulative experiments, and observations made in average and below-average precipitation years. Populations of *P. Jeffreyi* were also evaluated with respect to subsequent frequency of attack by a needle scale (Pine needle scale, *Matsucoccus bisetosus* Morrison) and bark beetle (Jeffrey pine beetle, *Dendroctonus jeffreyi* Hopk.), as well as tree mortality rates. This approach using C, water, and N balance attributes as measures of plant vigor and susceptibility to environmental change was evaluated over a period of nearly two decades.

2. Methods

2.1. Background

Data from three studies, conducted from 1991 to 2008, were drawn upon to address questions posed. The first study was coordinated through a Man and the Biosphere project (MAB) in 1991. It consisted of both a latitudinal and elevational transect on the western slope of the southern Cascade Range (Crater Lake National Park, CLNP, L43W (at a latitude "L" of 43°N; "W" to denote western slope of the Cascades or subsequent mountain range)), Sequoia National Park (SNP, L36W), San Jacinto State Park (SJSP, L34W), and San Pedro Martir National Park, Baja Norte, MX (SPMNP, L31W) (Fig. 1). Physiological measurements were made three to five times during the growing season in 1991 and included Pg, WUE, needle growth and retention, and foliar C and N. A total of 105 trees in the four species were sampled systematically through the summer.

The second study was conducted from 1997 through 2008 at a single site on the western slope of the southern Sierra Nevada, in Sequoia National Park (SNP, L36W). In July 1997, experimental measures of water use efficiency and early morning leaf water potentials were conducted in mid canopy of the four conifers. In 1998 through 2008, an extensive study was carried out to determine the interactive effect of N amendment (as a surrogate for excess N deposition) and microsite water availability on canopy health of *P. Jeffreyi*. Both descriptive (trees in mesic vs. xeric microsites at background deposition levels of 6–7 kg N ha^{-1} yr^{-1}, $n = 64$) and manipulative (amendment of 50 kg N ha^{-1} yr^{-1}, $n = 64$) studies were conducted. The data collected included gas exchange, canopy transpiration, needle retention and elongation, presence or absence of needle scale and bark beetle attack, and canopy health assessments. Background information on the level of drought stress experienced and response of canopy health attributes has been published previously (Grulke et al., 2003a,b).

The third study was conducted from 2007 to 2008 on a large latitudinal gradient on the eastern side of the following mountain ranges: the Transverse Range of southern California (San Bernardino National Forest, SBNF, L34E ("E" to denote eastern slope of mountain range)), the Sierra Nevada (Sequoia NF (L36E), Inyo NF (L38E), and Tahoe NF (L39E)), and the southern Cascade Mountains (Lassen NF (L41E)). Existing thin and dense stands, a south to north latitudinal gradient, and interannual differences in precipitation were used to drive differences in the level of tree drought stress experienced. There were 285 *P. Jeffreyi* in this study. The measures include pre-dawn and noon leaf water potential and component potentials, needle retention and elongation, and canopy health including presence or absence of needle scale and bark beetle attack.

2.2. Climatic constraints

The field sites were dominated by the mediterranean-type climate, of which 90% of the annual precipitation is received by April 15 (starting with the hydrologic year at October 1; see Grulke et al., 2009). Summer precipitation is usually not effective in increasing available soil water: it decreases whole system evapotranspiration for a couple of days, and then the seasonal drying trend resumes until approximately two weeks after the onset of autumn precipitation (Temple and Miller, 1998). Hydrological models are not particularly good at predicting drought stress in rocky, mountainous, mediterranean-type climates because the soil depth is highly variable (and unknown), the effectiveness of single rainfall events is unknown, and because trees depend on near-surface soil horizons for water in early season, then shift to lower soil horizons (cracks in bedrock) when the upper horizons dry: the volume of water in the bedrock is unknown. For this reason, defined physiological drought stress was linked to percent deviation from average annual precipitation at each site of interest. Data for annual precipitation were obtained from the National Weather Service and from county water districts.

2.3. Gas exchange

In 1991, gas exchange was measured on previous year, attached needles, on primary branches (in direct sun for at least 30 min, on the tree aspect with the greatest exposure (usually southern)), in six pole-sized (40–60 yr old) trees at each site and elevation over the growing season (3–5 sampling points). In 1997, gas exchange measures of the four species were conducted at a single location (Crystal Cave area) in SNP (L36W), in mid summer (July 14–27) on mature trees (100–120 yr old). Net assimilation was measured with a closed gas exchange system (Model 6200, LiCor Instruments, Lincoln, NE) in the 1991 study, and with an open gas exchange system (Model 6400, LiCor Instr.) in 1997 and subsequent years. A measure of respiration was conducted after each measure of net assimilation on the same needles during the daytime, using a dark acclimation period of 12–15 min, at a similar leaf temperature to that of net assimilation. Gross photosynthesis, Pg, was calculated from net assimilation plus daytime leaf respiratory losses. Because there is greater effect of temperature and endogenous metabolism on respiration vs. photosynthetic processes, Pg was believed to be a better measure than net assimilation (A) for comparing carbon acquisition across elevational and latitudinal gradients, and for populations with differing endogenous respiration rates. Leaf area was calculated geometrically from fascicle diameter and needle length (*Pinus*, spp., 6.1415*L*W) and from needle length and width (*A. concolor*, L*W*2).

Water use efficiency (WUE) was calculated from the ratio of concurrent measures of net assimilation and stomatal conductance in 1991 (spot measures), as well as experimentally determined as the slope of a line fit to four measures of gas exchange (A vs. gs) at different VPD_Ls on attached needles in mid canopy of mature trees in SNP (L36W) in 1997. Different VPD_Ls were obtained by varying flow through the desiccant (Model 6400, LiCor Instruments, Lincoln, NE). Equilibrium gas exchange measures were obtained at each VPD_L.

2.4. Leaf water potential

Leaf water potential was measured in early morning (between 0500 and 0600) from mid canopy in mid summer, 1997 for all four conifers in SNP (L36W). Needle xylem water potentials (Ψ_L) were determined on previous year's fascicles with a pressure chamber (PMS Inc., Corvallis, USA: Pallardy et al., 1991). Foliar water content of needles was also determined (([field weight − dry weight]/[dry weight])*100%). Dry weight of foliage was measured after 48 h at 65°C in a drying oven.

2.5. Elongation growth and needle retention

Needle and branch length by annual increments, and needle retention (number of needle age classes) were measured on 5 to 10 branches in the four MAB sites (1991, Fig. 1), 2–4 branches for all trees in SNP (L36W: 1997, 2006, 2007, 2008), and on 2 to 4 branches for all sites in the eastern Transverse Range, Sierra Nevada, and southern Cascade sites (L34E, L36E, L38E, L39E, L41E: 2007, 2008). Branches were sampled in mid canopy on the southern (or most exposed) canopy aspect, and needle and branchlet length for the prior 8 years were measured (see Grulke et al., 2003b). To estimate the level of drought stress, in a given year, of individual trees within the context of its microsite, elevation, and latitude, elongation growth was expressed as the % of the maximum needle or branchlet elongation growth observed on each secondary branch sampled.

2.6. Tissue chemistry

Foliage was sampled from 2 to 5 secondary branches, from mid canopy of the most exposed canopy aspect (generally southern) for all trees of each species in 1991. As soon as each branch was cut, previous year needles were subsampled around the branches, trimmed, placed in cryovials, flash frozen, transported in liquid nitrogen to the lab, and stored in a −80 °C freezer. They were then freeze-dried, ground, and analyzed on a Carlo-Erba 1500 C N S analyzer. Two standards were used: four quantities of atropine before and after

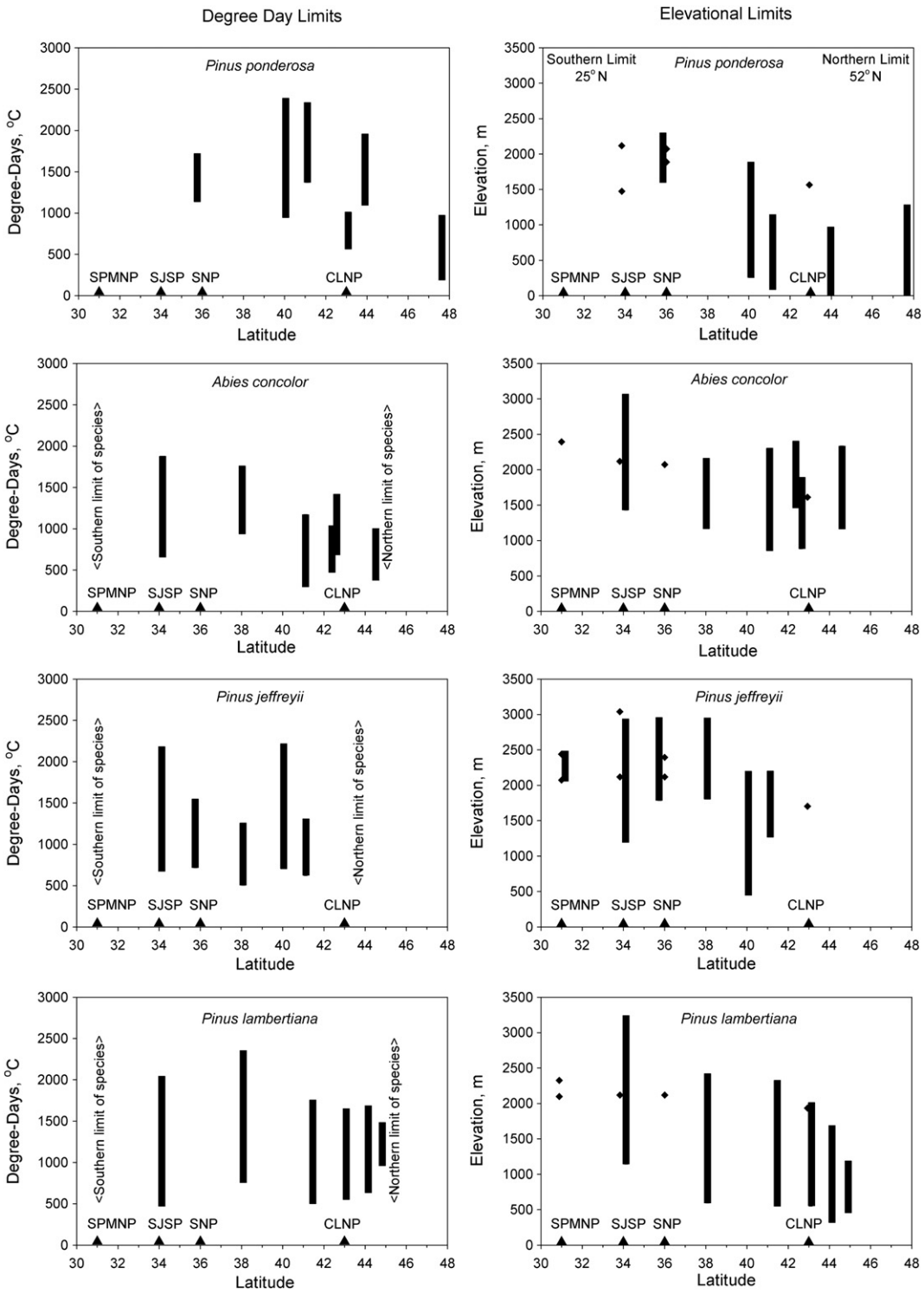

Fig. 1. Distributional and degree day limits of the four conifers, with a diamond marking sample locations used in this study (data provided by Dr. Dean Urban, Duke University). SPMNP denotes San Pedro Martir National Park, Baja Norte, MX; SJSP denotes San Jacinto State Park; SNP denotes Sequoia National Park; and CLNP denotes Crater Lake National Park.

each run, as well as a certified NITS pine needle standard every tenth sample. Replicates differed less than 5%.

2.7. Tree and canopy health

The presence of needle scale and Jeffrey pine beetle attack was assessed in SNP (L36W) (biennially from 1998 through 2008), and in east side Jeffrey pine stands in the SBNF (L34E), SNF (L36E), INF (L38E), TNF (L39E), and LNF (L41E) (2007, 2008). In 2006, tree boles were examined for evidence of Jeffrey pine beetle entrance and exit holes by John Wenz (Entomologist, retired, USDA Forest Service, Sonora, CA), and for foliar pathogens by John Pronos (Plant Pathologist, retired, USDA Forest Service, Sonora, CA) in SNP (L36W). Needle pathogens, Jeffrey pine beetle, and pine needle scale were recorded in subsequent surveys by the author. Tree mortality and its cause, if discernable, was recorded biennially from 1998 through 2008 in SNP.

2.8. Statistical analysis

Differences in physiological attributes among species were tested with a 1-way analysis of variation. Differences in physiological attributes between years, stands of differing densities, and with and without Jeffrey pine beetle attack were tested with

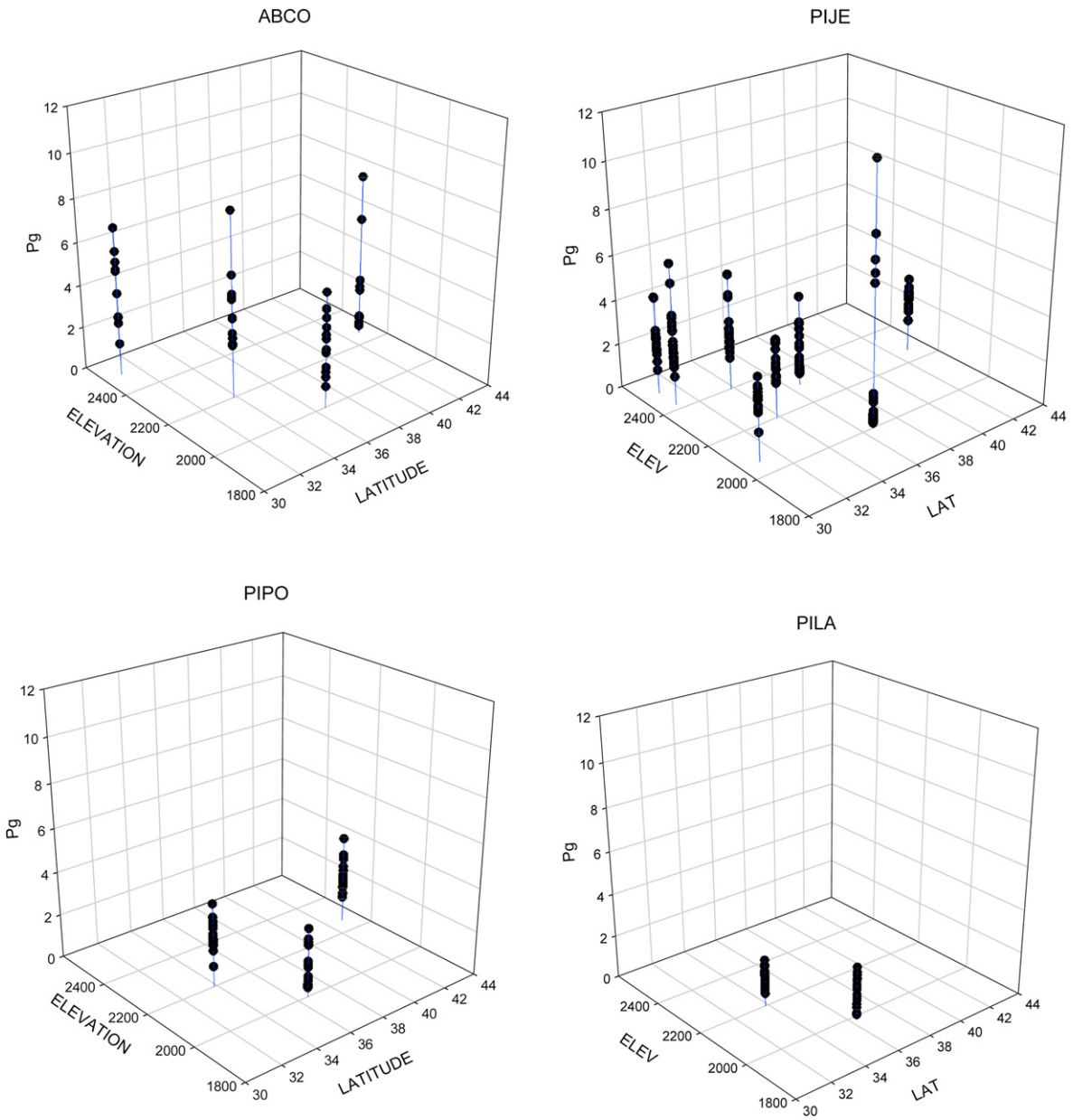

Fig. 2. Variation in gross photosynthesis, Pg (net assimilation + dark respiratory losses) of the four conifers, *Abies concolor* (ABCO), *Pinus lambertiana* (PILA), *P. ponderosa* (PIPO), and *P. Jeffreyi* (PIJE). Each point represents the average foliar gas exchange measures of several fascicles (or approximately 10 needles of *A. concolor*) measured mid-morning.

1- and 2-way analyses of variation (SigmaplotSoftware 11.0). Within the text, significance was reported when $P < 0.05$. There were no statistical analyses performed on data as presented in Figs. 4 and 5.

3. Results

3.1. Gross photosynthesis

As measured over the growing season, Pg was the lowest and the least variable for *P. lambertiana* relative to the other three conifers (Fig. 2). The range of Pg exhibited by *P. ponderosa* was intermediate between *P. lambertiana* and *P. Jeffreyii*. *P. Jeffreyi*, and *A. concolor* exhibited considerable variability in Pg within most sites sampled, with the greatest range in Pg at the northernmost site (CLNP, L42W) for both species. Populations of *P. Jeffreyii* exhibited the lowest values and least variability in Pg at a low elevation location of the species at SNP (L36W), and at the lowest elevation and latitude site (SPMNP, L31W). At all latitudes, Pg of *P. Jeffreyi* had lower values at the lowest elevation sites.

As a component of Pg, *A. concolor* had the highest daytime foliar respiration, with the highest range and values in the three southern latitude sites (L31W, L34W, L36W; Fig. 3). Foliar respiration of *A. concolor* at the northernmost site (L43W) was half that (0.11–0.75 μmol m^{-2} s^{-1}) of the southernmost latitude (L31W) (0.44–1.65 μmol m^{-2} s^{-1}). Foliar respiration of *P. ponderosa* had consistent, high variability across all latitudinal sites sampled (0.03–1.21 μmol m^{-2} s^{-1}). *P. Jeffreyi* exhibited intermediate values (less than *A. concolor* and *P. ponderosa*, but greater than that of *P. lambertiana*); foliar respiration at the higher elevation sites was lower by ca. 0.10 μmol m^{-2} s^{-1}. Foliar respiration of *P. lambertiana* was the lowest and least variable of the four conifers measured (0.04–0.48 μmol m^{-2} s^{-1}).

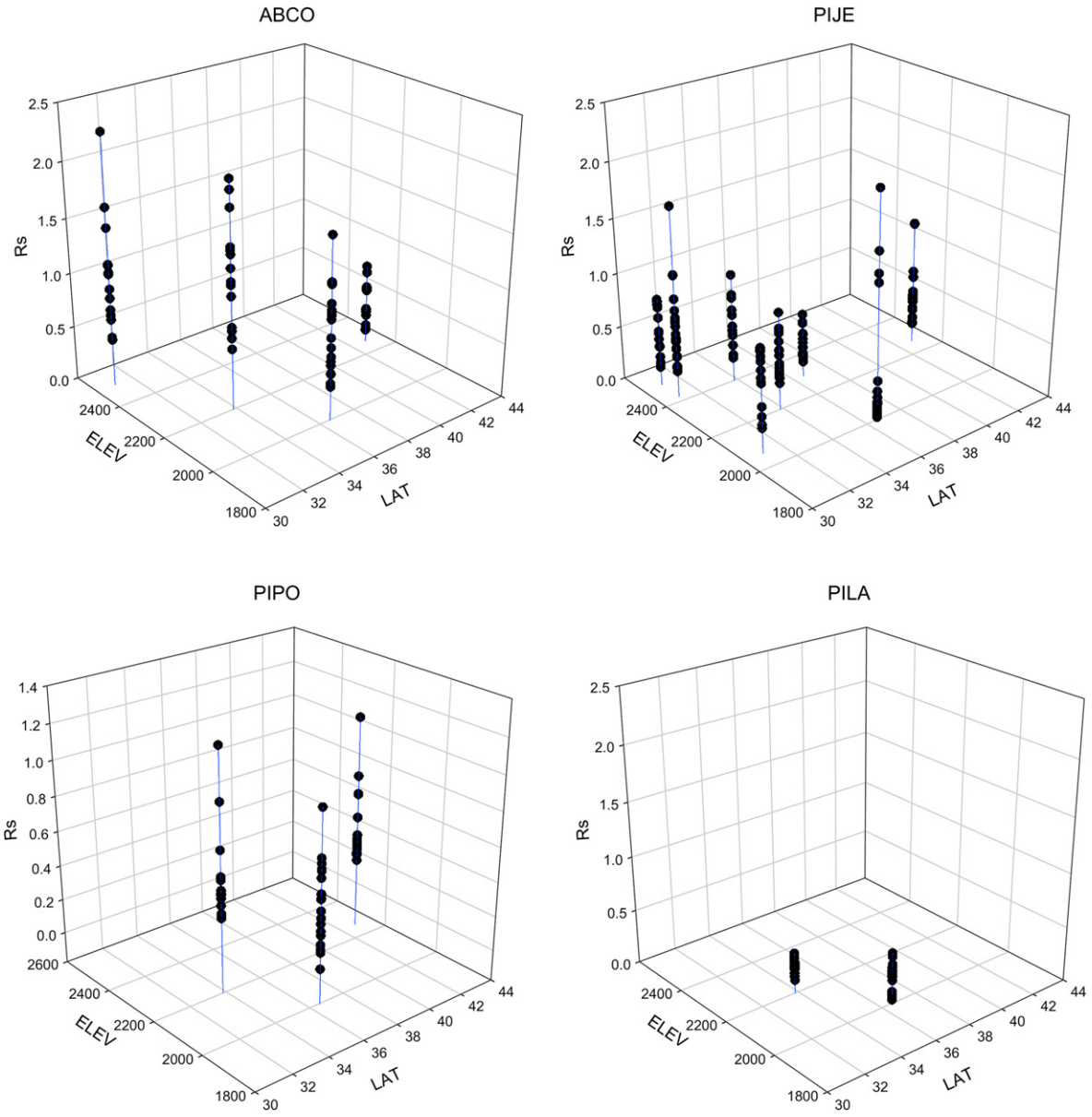

Fig. 3. Variation in daytime foliar respiration (Rs) across a latitudinal and elevational gradient for the four conifer species. Acronyms as in Fig. 2.

3.2. Water use efficiency

All four conifers had similar average late summer leaf-level WUE (Table 1). However, within a species, leaf-level WUE may differ from early to late growing season. In early growing season, soil water is less limiting, carbon stores are low due to overwintering losses and demands for new growth provide a large sink for carbon. During this time, photosynthetic carbon gain is high and stomatal conductance is less likely to limit assimilation. WUE can be significantly lower early in the growing season relative to late in the growing season. This was the case for both *P. ponderosa* and *A. concolor* (Table 1), suggesting a greater degree of within-growing season plasticity. For these two species, only the more efficient, late season WUE was included in Fig. 4. For *P. Jeffreyi* and *P. lambertiana,* WUE did not differ significantly within the growing season, and all measures taken over the growing season were included in graphed points.

P. lambertiana exhibited the lowest values and least variability in WUE (Fig. 4). *P. Jeffreyi* exhibited high variability in WUE within a site, but little difference in either value or range among sites. *P. ponderosa* and *A. concolor* had similar high WUE, and higher variability in WUE at the northernmost latitude (CLNP). The maximum observed WUE declined from northern to southern latitudes, with a marked decrease in variability in the southernmost population of *P. ponderosa* (SJSP, L34W). For *A. concolor,* WUE was consistent in value and level of variability at the three lower latitude sites (SNP (L36W), SJSP (L34W), and SPMNP (L31W)). Based on these seasonal measures, taken in a functionally dry year[2], the rank order of WUE among the four conifers was *P. Jeffreyi* = *P. lambertiana* > *P. ponderosa* = *A. concolor* (Table 1, A).

[2] In southern California, 1991 received 91% of the long-term average precipitation, although 60% of the annual precipitation was received in a single month, much of which was likely to have been lost as overland flow. SNP received 81% of the long-term average precipitation.

Table 1
Summary of attributes of water handling capacity of the four conifers, *Pinus Jeffreyi* (PIJE), *P. ponderosa* (PIPO), *P. lambertiana* (PILA), and *Abies concolor* (ABCO). Water use efficiency was determined from gas exchange measured over the growing season (A, 1991) and from experimental manipulations in July, 1997 (B, at site L36W). The slope of the linear relationship between stomatal conductance (gs, mmol m^{-2} s^{-1}) and leaf water potential ((C) Ψ_L, MPa) and leaf to air vapor pressure deficits ((D)VPD_L, kPa), listing significant correlation coefficients (R; or n.s. indicating no significance). Average early morning Ψ_L is presented in (E). Different letters denote significant differences at $P < 0.05$ level within a species between sampling dates (A, first letter, subscript 1) or among species (A, second letter, subscript 2; E). Incomplete data sets are indicated by "i.d."

A. Spot measures of water use efficiency (*A*/gs):		
	June	August
PIJE	$0.112 \pm 0.003a_1a_2$	$0.117 \pm 0.004a_1a_2$
PILA	$0.099 \pm 0.010a_1a_2$	$0.110 \pm 0.004a_1a_2$
PIPO	$0.089 \pm 0.004a_1b_2$	$0.111 \pm 0.005b_1a_2$
ABCO	$0.083 \pm 0.008a_1b_2$	$0.109 \pm 0.004b_1a_2$
B. Experimentally derived water use efficiency (*A*/gs)		
PILA	0.087	$R = 0.90$
PIPO	0.077	$R = 0.88$
ABCO	0.068	$R = 0.75$
PIJE	0.062	$R = 0.83$
C. Rate of change in gs with decreasing Ψ_L		
ABCO	−114	$R = 0.92$
PIJE	−12	$R = 0.60$
PILA	−9	n.s.
PIPO	i.d.	i.d.
D. Rate of change in gs with increasing VPD_L		
ABCO	−26.6	$R = 0.98$
PILA	−13.4	$R = 0.98$
PIPO	−9.4	$R = 0.98$
PIJE	−6.5	$R = 0.98$
E. Early morning Ψ_L (MPa)		
PILA	-1.6 ± 0.5a	
ABCO	-2.0 ± 0.2ac	
PIJE	-2.3 ± 0.4ac	
PIPO	-2.3 ± 0.1bc	

Based on experimentally derived measures of WUE (driven by incremental changes in VPD_L with equilibration at each value), the rank order from highest to lowest of the four conifers was *P. lambertiana* > *P. ponderosa* > *A. concolor* > *P. Jeffreyi* (B; Table 1). These data were taken in an above average precipitation year preceded by the same in SNP (L36W). *P. lambertiana* appears to have the lowest plasticity based on lack of variability in WUE between sites, and low WUE under drought conditions (1991).

3.3. Stomatal responsiveness to leaf Ψ

Another measure of relative plasticity among species is the rate of change in gs with changing environmental conditions, presented here for leaf water potential and VPD_L. Of the conifers measured, *A. concolor* had the greatest rate of stomatal closure with decreasing Ψ_L (C; Table 1). *P. Jeffreyi* and *P. lambertiana* had low rates of stomatal closure in response to Ψ_L. *P. lambertiana* had the most favorable early morning leaf water status of the four species (E; Table 1). The rank order of Ψ_L during mid summer, 1997 was *P. lambertiana* > *A. concolor* = *P. Jeffreyi* > *P. ponderosa*. Stomatal closure of *A. concolor* was very responsive to increasing VPD_L relative to the other species assessed in this study (D; Table 1). Although the rate of stomatal closure in response to decreasing Ψ_L was higher for *P. Jeffreyi* relative to *P. lambertiana*, stomatal closure in response to atmospherically unfavorable conditions (as imposed by increasing VPD_L) was greater for *P. lambertiana*, then *P. ponderosa*, followed by *P. Jeffreyi*. Percent leaf moisture ranged from 225 to 235% and did not differ significantly among the four species (data not presented).

3.4. Needle retention and elongation growth

A. concolor had the greatest needle longevity in mid latitudes, with significant loss in needle retention at both the lowest and highest latitudes sites (Table 2). *P. Jeffreyi* had the opposite pattern, with the lowest needle retention at the mid-latitude sites (at mid elevation). *P. lambertiana* had the highest needle retention at its lowest latitude site (SJSP, L34W). *P. ponderosa* had no significant variation in needle retention across the latitudinal gradient (at mid elevation).

Needle elongation was the greatest at the most southern latitude for both *P. lambertiana* and *P. Jeffreyi* (SPMNP, L31W; Table 2). There was no difference in average needle elongation for *P. ponderosa* among sites.

Needle retention and elongation was evaluated for both latitudinal and elevational gradients for *P. ponderosa* and *P. Jeffreyi* (Fig. 5). Whorl retention was greatest at the lowest latitude, mid elevation site (SPMNP, L31W) or the highest elevation site (all other latitudes) for both species. For *P. Jeffreyi*, needle elongation was the greatest at the lowest elevation site at all latitudes. For *P. ponderosa*, needle elongation was only lower at the mid elevation site at SNP (L36W).

Needle elongation of *P. Jeffreyi* in mesic microsites with or without N amendment did not significantly differ between years of 57% and 92% of the long-term average precipitation at SNP (L36W) (Table 3; Grulke et al., 2003a). In xeric microsites, needle elongation of *P. Jeffreyi* was significantly greater in the year with more available soil water (5% greater). With N amendment, needle elongation growth was 11% greater than that with background N deposition in the year with greater precipitation.

For sites that had greater precipitation in 2008 than 2007 (SBNF (L34E), SNF (L36E), INF (L38E)), there were significant increases in needle elongation in *P. Jeffreyi* relative to elongation growth in the below-average precipitation year, 2007 (Table 4). There was no difference in precipitation in 2007 and 2008 at TNF (L39E), but there were still significant increases in needle elongation in 2008. At LNF (L41E), total annual precipitation was lower in 2008 than 2007, but there were no significant differences in needle elongation between the years, within the same stand density. At higher latitudes (>L34E), needle elongation of *P. Jeffreyi* was greater in thin (vs. dense) stands. At the southern latitude (SBNF (L34E)), *P. Jeffreyi* in dense stands had higher needle elongation growth than trees in thin stands, perhaps due to increased canopy evapotranspiration in thin stands. In years of greater precipitation, needle elongation growth was greater in thin stands.

3.5. Foliar chemistry

Foliar nitrogen (N) of *A. concolor* was much higher across all needle age classes at the highest latitude site (L43W) than that at any other more southern latitudes (Fig. 6). The next highest % foliar N occurred at the southernmost latitude (SPMNP, L31W), which was 0.1–0.3% greater than that of the middle latitude sites. Among the pines, *P. Jeffreyi* had the highest % foliar N by 0.4%. Trees at the southernmost latitude (SPMNP, L31W) had the highest % foliar N, followed by trees at the northernmost latitude. The % foliar N of all three pines was the lowest at SNP (L36W). There was little difference in % foliar N of *P. ponderosa* at any latitude. Although there was little difference in foliar N in most needle age classes (3–5 yr old needles) of *P. lambertiana*, the youngest needle age classes (1 and 2 yr old) had lower N content at SJSP (L34W) than at CLNP (L43W), whereas the opposite was true for the oldest needles (6 yrs old).

Percent foliar C of *A. concolor* was similar among sites and was consistently maintained across all needle age classes except for at SJSP (L34W), which was lower by 4% from all other sites from the

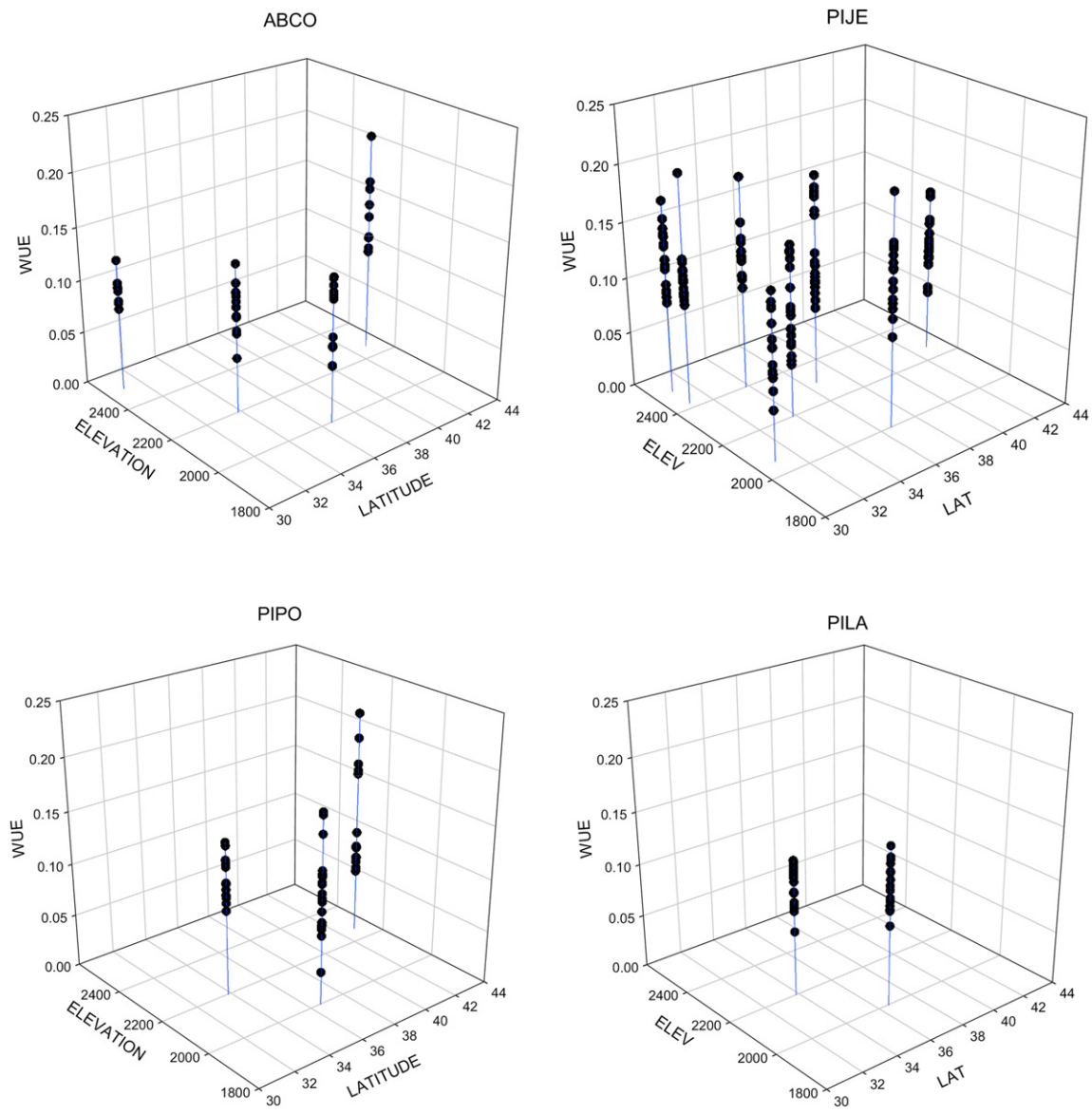

Fig. 4. Variation in water use efficiency (A/gs, WUE) with latitude and elevation among the four conifer species. Acronyms as in Fig. 2.

4th through the 18th needle age class (Fig. 6). At SJSP (L34W), the C content of needles declined asymptotically from current year foliage to the 18th needle age class. In *P. Jeffreyi*, % foliar C was highest at SPMNP (L31W), followed by SNP (L36W). At these two sites, % foliar C increased predominantly from current to 3 yr old needles. Percent foliar C in this species was lowest at SJSP (L34W) and CLNP (L43W), and C content increased between 3 and 6 yr old needles. *P. lambertiana* had a similar pattern of increased C content with needle age, but C content was highest at SNP (L36W). Percent foliar C of *P. ponderosa* was the highest, and consistently high across all needle ages at its southernmost distribution in California (SJSP, L34W). Percent foliar C at SNP (L36W) and CLNP (L43W) had significantly lower C content at all needle ages; foliage at SNP (L36W) had a significant increase in C content in the 5th through the 8th needle age classes.

3.6. Pathology

Among the east side Sierra Nevada sites, needle scale was observed on intensively studied trees only at Lassen NF in 2007 and 2008 (L41E, Table 4), the only site with two sequential years of below 60% of average precipitation and depressed needle elongation growth. The frequency of needle scale was 0.09 in thin stands, and 0.23 in dense stands. Needle scale also occurred on the western

Table 2
Summary of needle longevity, and maximum needle elongation growth (in mm) for the four conifers at mid elevation in the four sites: San Pedro Martir National Park (SPMNP, L31W), San Jacinto State Park (SJSP, L34W), Sequoia NP (SNP, L36W) and Crater Lake NP (CLNP, L43W). Rows with different letters denote significant differences within a species, among sites at the $P < 0.05$ level.

	SPMNP	SJSP	SNP	CLNP
Number of needle age classes				
A. concolor	12.7 ± 0.2a	15.3 ± 0.3b	14.1 ± 0.2c	11.8 ± 0.2d
P. lambertiana		7.3 ± 0.2a	5.2 ± 0.1b	5.0 ± 0.1b
P. Jeffreyi	6.3 ± 0.1a	5.6 ± 0.1b	4.4 ± 0.1c	6.3 ± 0.1a
P. ponderosa		6.8 ± 0.2a	6.8 ± 0.1a	6.6 ± 0.1a
Needle elongation				
P. lambertiana		44 ± 2a	36 ± 1b	34 ± 2b
P. Jeffreyi	80 ± 4a	74 ± 5a	71 ± 4a	65 ± 1b
P. ponderosa		82 ± 7a	82 ± 3a	86 ± 2a

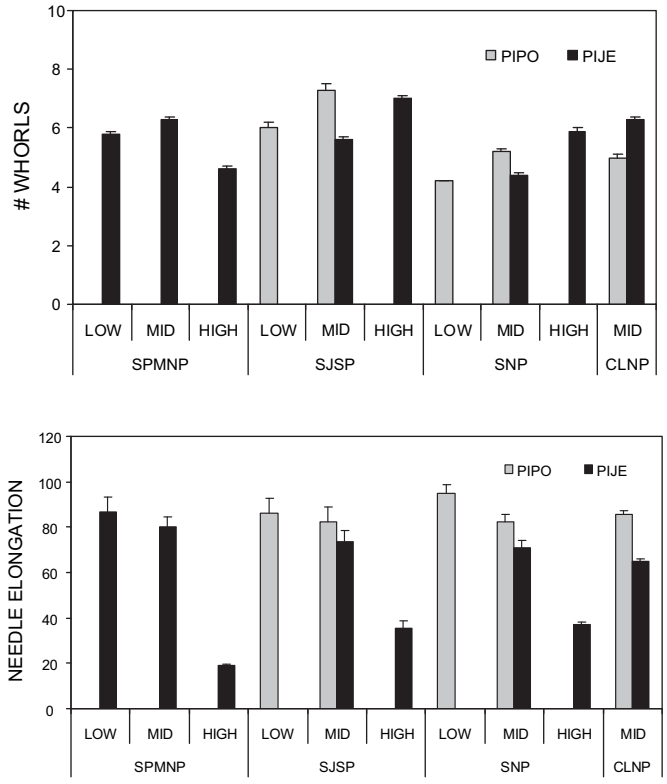

Fig. 5. Comparison of whorl retention (upper graph) and needle elongation (lower graph) between the two closely related species of yellow pine (*P. ponderosa* and *P. Jeffreyi*) on both elevational and latitudinal gradients. Bar height represents mean of 5 trees per species (±1 S.E.). From southern to northern latitudes: San Pedro Martir National Park (SPMNP, L31W), San Jacinto State Park (SJSP, L34W), Sequoia National Park (SNP, L36W), and Crater Lake National Park (CLNP, L43W).

slope of the Sierra Nevada at SNP (L36W). Needle scale was more frequent in trees growing in xeric vs. mesic microsites (Table 3). Eight years of N amendment (50 kg N ha yr^{-1}) increased needle scale frequency in mesic microsites but decreased scale frequency in xeric microsites (relative to trees with only background N deposition).

Trees attacked by Jeffrey pine beetle were present in the general area of all eastern Sierra Nevada sites assessed in 2007 and 2008, either within or adjacent to established plots. Trees within plots have died due to Jeffrey pine beetle (2% among the thin plots at SNF (L36E) and 9% among the thin plots at LNF (L41E)). On the western slope of the Sierra Nevada in SNP (L36W), trees in xeric microsites with background N deposition had the highest mortality (22%), followed by trees in xeric microsites with N amendment for 8 years (9%) and trees in mesic microsites with N amendment (9%). The mortality of all of these trees was attributable to Jeffrey pine beetle (John Wenz, personal communication, 2006). There was no mortality in trees due to Jeffrey pine beetle in mesic microsites at background N deposition over a decade of monitoring.

Table 3
Effect of an 8 yr background N, and N amendment manipulation of Jeffrey pine on the west slope of the Sierra Nevada (L36W). Needle elongation growth has been reported for a drought year (2007, 57% of 86 yr average) and a year of average precipitation (2008; 92% of average). The frequency of needle scale was reported from 2008, and decadal mortality rates (1998–2008). All tree mortality was attributed to successful Jeffrey pine beetle attack in 2006 by John Wenz (personal communication, Entomologist, retired, USDA FS) and in 2008 by the author. Dissimilar letters denote statistically significant differences within a treatment between years at the $P < 0.05$ level.

	MESIC control	MESIC +N	XERIC control	XERIC +N
Needle elongation				
2007	85 ± 1a	84 ± 1a	82 ± 1a	80 ± 1a
2008	88 ± 2a	86 ± 1a	86 ± 2b	89 ± 1b
Needle scale, freq	0.06	0.16	0.28	0.17
Decadal mortality	0	9.4%	21.9%	9.4%

4. Discussion

In this study, the range in values of ecophysiological traits of four co-occurring conifers, *A. concolor*, *P. Jeffreyi*, *P. ponderosa*, and *P. lambertiana*, were compared across a large latitudinal gradient to improve understanding of their potential to respond to changing environmental conditions. Of the four species studied, *P. lambertiana* had the least variability in traits, and lowest Pg and % foliar N of young needle age classes, especially at SJSP (L34W) and SNP (L36W). The data presented here suggests that *P. lambertiana* populations are likely to be vulnerable to environmental change due to low apparent variability of key traits. There is little ecophysiological data on this species with which to compare. A measure of foliar $\delta^{13}C$ indicated that the integrated foliar WUE of this species was greater than that of *P. ponderosa* (Zimmer et al., 2007), supporting both the field survey as well as steady state determinations of WUE (Table 1). In an evaluation of bole wood structure, Jagels (2006) described diffuse transition between early and late wood in *P. lambertiana*, suggesting a slow depletion of available soil moisture. The wood anatomy supports the lack of difference in early vs. late season WUE, tight stomatal control, and maintenance of relatively high Ψ_L (Table 1) (*sensu* McDowell et al., 2008). Van Mantgem and Stephenson (2007) reported greater mortality in *Pinus* than in *Abies* (10% vs. 3%, respectively), but mortality below the genus level of *Pinus* was not reported. The mortality was attributed to both abiotic and biotic stresses, but largely to a temperature-driven increase in an index of drought. Because trees access deep water in the interstices of weathered bedrock, it is likely that the temperature-driven increase in the drought index largely influences evapotranspirational water loss, affecting *P. Jeffreyi* more than *P. ponderosa* and *P. lambertiana* based on data presented in Table 1. Mortality of *P. lambertiana* succumbed to white pine blister rust in the mid 1970's to 1980's (Kinloch and Dulitz, 1990). Because of this large selection factor, *P. lambertiana* may already have reduced genetic diversity in the surviving populations.

Of the four conifers, *A. concolor* and *P. Jeffreyi* had the most variability in key ecophysiological traits. For *A. concolor*, the greatest variability was observed at the highest latitude site. Although *A. concolor* ranked the lowest in a field survey of spot measurements of WUE, and second to lowest in WUE as determined under steady state conditions, this species had the most responsive stomata to dynamic changes in both Ψ_L and VPD_L (Table 1). *A. concolor* responded much more quickly to changes in Ψ_L (10× greater than *P. Jeffreyi* and *P. lambertiana*), and VPD_L (2× greater than *P. lambertiana*, 3× greater than *P. ponderosa*, and 4× greater than *P. Jeffreyi*). Both *A. concolor* and *P. Jeffreyi* had lower WUE in early summer when water was ample to higher WUE in late summer when water availability was restricted, maximizing growth rates under both conditions (see discussion in Picotte et al., 2007).

Early morning Ψ_L of *P. lambertiana*, *A. concolor*, and *P. Jeffreyi* reported in this study (measured in July, 1997 in SNP) were very similar and had the same rank order as pre-dawn Ψ_L reported by Royce and Barbour (2001; pooled measurements in 1994 and 1995 in the Kern Plateau 70 km south of SNP). Based on a long-term precipitation record in SNP, 81% of the average was received in

Table 4
Needle retention (# whorls), needle lengths in 2007 and 2008, in mm, % of average precipitation relative to long-term precipitation record at each site, and the frequency of needle scale in Jeffrey pine on the eastern slope of the Transverse Range (SBNF), Sierra Nevada (SNF, INF, TNF) and Cascade Range (LNF). Comparison of secondary branch morphological attributes between within-site, paired trees with and without Jeffrey pine beetle (JPB) attack at a site (TNF 2) just west of TNF 1. Dissimilar letters denote statistically significant differences at the $P < 0.05$ level between trees in thin and dense stands (e.g., a_1, b_1), and for the same trees measured in both 2007 and 2008 (e.g., a_2, b_2). The significance of the interaction term between stand density and year (YR) is given in the column ANOVA ('–' indicates no significant interaction; 'NA' indicates not applicable). There were 24 trees in each stand type (thin, dense).

	2008	2007	2007	2008	2008	2008	Stand density × YR
	# Whorls	Needle length	PPT, %	Needle length	PPT, %	Needle scale	
SBNF (L34E)							
THIN	$5.7 \pm 0.1a_1$	$29 \pm 3a_1a_2$	31	$66 \pm 2a_1b_2$	95	0	<0.001
Dense	$5.9 \pm 0.2b_1$	$48 \pm 4b_1a_2$		$55 \pm 3b_1a_2$		0	
SNF (L36E)							
Thin	$6.8 \pm 0.2a_1$	$38 \pm 3a_1a_2$	66	$72 \pm 2a_1b_2$	79	0	–
Dense	$6.4 \pm 0.2a_1$	$29 \pm 2b_1a_2$		$68 \pm 2a_1b_2$		0	
INF (L38E)							
Thin	$6.9 \pm 0.2a_1$	$61 \pm 2a_1a_2$	33	$76 \pm 2a_1b_2$	60	0	–
Dense	$6.3 \pm 0.3b_1$	$47 \pm 4b_1a_2$		$69 \pm 2a_1b_2$		0	
TNF 1 (L39E)							
Thin	$6.2 \pm 0.1a_1$	$61 \pm 2a_1a_2$	58	$75 \pm 2a_1b_2$	58	0	–
Dense	$6.6 \pm 0.2b_1$	$50 \pm 3a_1a_2$		$71 \pm 2a_1b_2$		0	
LNF (L41E)							
Thin	$5.6 \pm 0.1a_1$	$73 \pm 1a_1a_2$	63	$73 \pm 1a_1a_2$	49	0.09	–
Dense	$5.4 \pm 0.2a_1$	$61 \pm 3b_1a_2$		$61 \pm 3b_1a_2$		0.23	
TNF 2 (L39E)							
NO Attack	$5.8 \pm 0.1a_1$	$74 \pm 1a_1a_2$	58	$72 \pm 2a_1a_2$	58	0.09	NA
JPB Attack	$6.2 \pm 0.3a_1$	$59 \pm 6b_1a_2$		$66 \pm 4a_1a_2$		0.30	

1997, and 1994 and 1995 were years of 66% and 140% of the average. It is likely that the precipitation patterns obtained for SNP (L36W) were regionally representative.

A. concolor had normally distributed needle retention with latitude, with the highest needle retention in the mid-latitude sites (L34W, L36W). The highest branch elongation growth and the highest % foliar C occurred at the lowest (L31W) and the highest latitudes (L43W), with lower values for each at the mid latitudes. All four species exhibited depressed needle growth and % foliar N at the mid-latitude site SNP (L36W), which may be a response to moderately high ozone (O_3) exposure (Staszak et al., 2007). Although *A. concolor* is asymptomatic, a physiological process model (parameterized with an independent data set) predicted a reduction in C stores, and subsequently reduced branch growth, with moderate O_3 exposure (Retzlaff et al., 2000). A similar effect on net assimilation was demonstrated in mature *P. ponderosa* using the same model (Grulke and Retzlaff, 2001).

Despite its restricted geographic range relative to *A. concolor* and *P. ponderosa* (Burns and Honkala, 1990), *P. Jeffreyi* had high variability in key ecophysiological traits, and exhibited the greatest needle and branch elongation growth in the driest site (SPMNP, L31W). For both *P. Jeffreyi* and *P. ponderosa,* the highest needle retention occurred in the mid elevation sites, at each latitude. However, needle elongation growth was highest for *P. Jeffreyi* at the southernmost site (SPMNP, L31W) at the lowest elevation, where *P. Jeffreyi* is invading an *Arctostaphylos*, spp. dominated shrubland (Minnich and Franco-Vizcaino, 1998). *P. ponderosa* does not occur this far south in the Peninsular Range, and in subsequent years, had significant mortality at its southern limit in this range due to an extended chronic (1999, 2000, 2001) and acute (2002) drought (Grulke et al., 2009).

At CLNP (L43W), *P. Jeffreyi* had restricted variability both in Pg and WUE. At SNP (L36W), *P. Jeffreyi* had very low values of WUE, as well as highly restricted variability in WUE. Nearly two decades later, both needle scale and Jeffrey pine beetle had significant infestations at SNP (L36W) and at a site south of CLNP at LNF (L41E, northern latitude site of the 2007, 2008 study). Although % foliar N of *P. Jeffreyi* was lowest at SNP (L36W), % foliar C was relatively high. Despite depressed Pg, it may be that the O_3 concentrations are high enough at SNP (L36W) that sugar transport out of the needles is limited, thus increasing C content (see Grantz and Farrar, 1999). Nonetheless, low resource availability may be the fundamental ecophysiological basis for tree susceptibility to successful bark beetle attack: low Pg, low WUE, and low foliar N. *P. Jeffreyi* trees that were successfully attacked by Jeffrey pine beetle had lower needle elongation growth relative to adjacent, unattacked trees (Table 4). Needle elongation growth in a given year, when expressed as a percent of the maximum needle length on the branchlet, was a proxy for tree drought stress experienced in the same year.

In general, needle elongation growth was lower in dense vs. thin stands of *P. Jeffreyi*, suggesting more drought stress in the dense stands. At one site (SBNF, L34E) within 5 km of the ecotone between the Mojave desert and pine-dominated mixed conifer forest, needle elongation growth was higher, not lower in the dense stands. At this site with high evaporative demand, close proximity of canopies may locally increase humidity and reduce evaporative losses from the canopy in dense stands.

Although greater mortality would be expected in dense stands, 2% mortality was observed within the thin stands at SNF (L36E) and 9% mortality was observed within thin stands at LNF (L41E). In stands where bark beetle attacks occurred, the probability of an attack for trees near other attacked trees was greater in thinned plots, so that thinning may not confer protection during large outbreaks (Preisler and Mitchell, 1993).

High N amendment (simulating high N deposition) increased needle scale (from 6 to 16%) and tree mortality due to Jeffrey pine beetle attack (from 0 to 9%) in trees in mesic microsites at a site with moderate to moderately high O_3 exposure (SNP, L36W). A similar study conducted in a *P. ponderosa*-dominated stand with high O_3 exposure and a background of ca. 40 kg N ha^{-1} yr^{-1} reported a 10% increase in tree mortality over a 6-yr period (1997–2003; Eatough-Jones et al., 2004). The total annual precipitation reported for the western San Bernardino Mountain site was comparable to SNP (L36W), but likely had a different site water

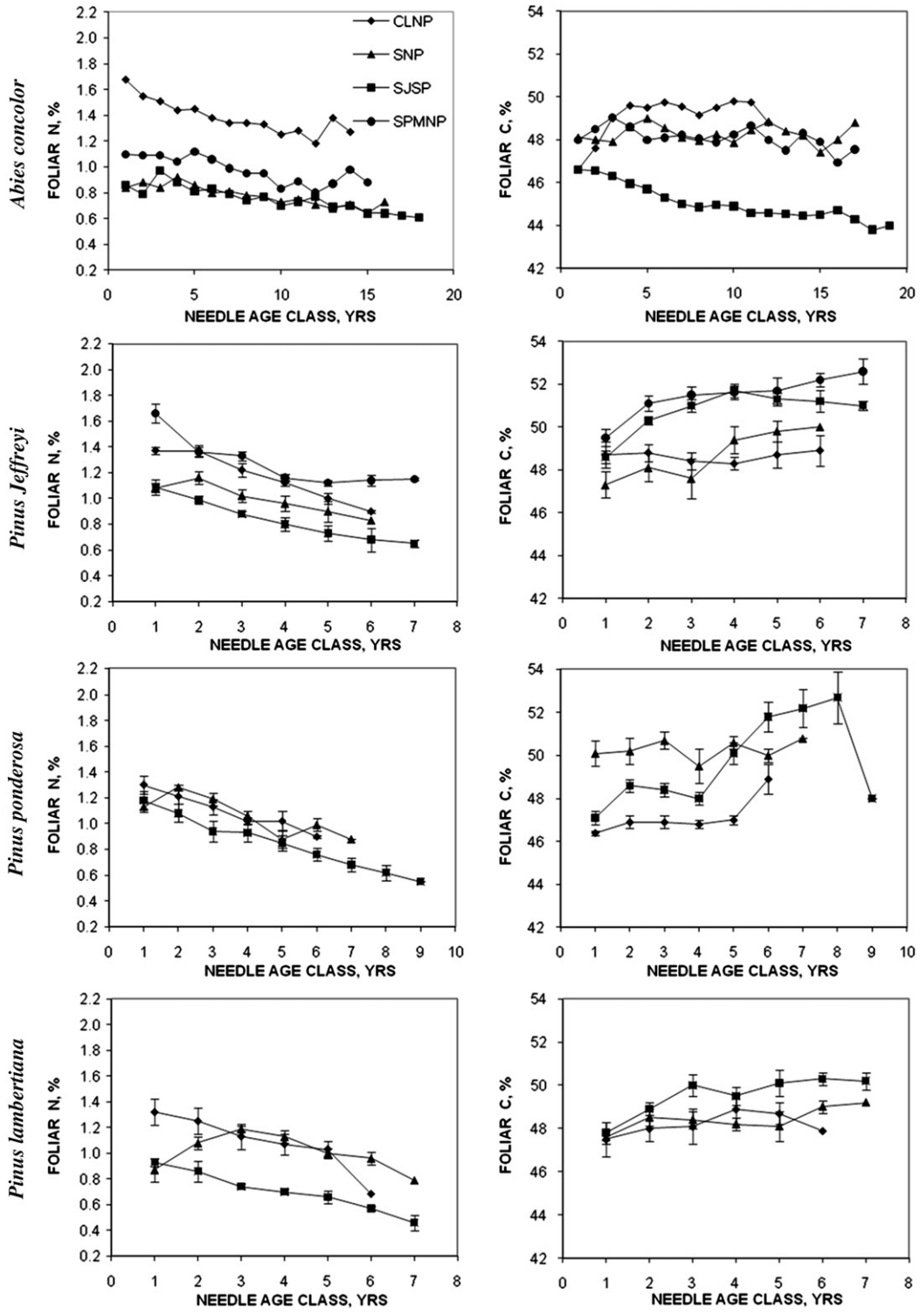

Fig. 6. Foliar nitrogen (N) and carbon (C) content (% of dry weight) for the four conifers at mid elevation in the four sites in early summer. Symbol represents mean of 5 plants ± 1 S.E.

balance due to frequent morning fog in the western SBNF (L34W) from early to mid summer. In a mixed age class, mixed composition (*P. ponderosa*/*P. Jeffrey*[3]) stand at the eastern end of the San Bernardino Mountains (L34E), tree mortality was 0% in background N deposition plots (6–9 kg N ha^{-1} yr^{-1}), and 2% in N-amended plots (background + 50 kg N ha^{-1} yr^{-1}) (Eatough-Jones et al., 2004). If the Eatough-Jones et al. (2004) results can be compared to the SNP (L36W) xeric microsites with a similar background N deposition level, the mortality reported for a 6 year period was much lower than that at SNP (L36W): the same high N amendment over

[3] 49%:51% *P. jeffrey*:*P. ponderosa* mix in background and background + 50 kg N ha^{-1} yr^{-1} plots.

a similar time period reduced both needle scale frequency (0.28–0.17) and decadal tree mortality (22%–9%) relative to trees with only background N deposition (Table 3).

Tree mortality in the mixed conifer forest of California was assessed in over 20,000 trees over two decades of monitoring (Van Mantgem and Stephenson, 2007). This study elucidates some of the underlying ecophysiological attributes that could have contributed to mortality in their study, as well as corroborates their mortality rates, albeit with a much smaller data set. The increase in mortality was attributed to increased temperature in their study. A study in the Peninsular Range in southern California showed that a temperature increase of 0.8 °C as well as episodic effects of the 1999–2002 drought resulted in an asymmetrical uphill 'lean' of vegetation zones (Minnich and Franco-Vizcaino, 2009). Because conditions of unfavorable water status are more common than 'favorable' in this mediterranean-type climate, the faster stomatal response to unfavorable environmental conditions observed in *A. concolor* is likely to result in increased water conservation relative to *P. Jeffreyi*. Kelly and Goulden (2008) reported a 96 m uphill change in mean elevational distribution of *A. concolor* over the last 30 years. On the same transect, they reported only a 28 m uphill shift of *P. Jeffreyi*. Although no net elevational change was observed at the lower elevational range in their study, an expansion downward might be predicted based on % foliar C, and needle elongation of lower elevation populations of *P. Jeffreyi* in this study (Figs. 5 and 6).

Of the four species characterized in the mixed conifer forest, *A. concolor* exhibited the greatest variability in key ecophysiological traits as well as dynamic stomatal responses to changes in both Ψ_L and VPD_L across a large latitudinal gradient. Documentation of uphill redistribution of *A. concolor* in the Peninsular Range of southern California further supports the capacity of this species to respond to environmental change (Kelly and Goulden, 2008). Despite its current restricted range (relative to *P. ponderosa* and *A. concolor*), *P. Jeffreyi* also exhibited significant variability in key traits, as well as high needle elongation growth at the margins of its latitudinal and elevational limits. However, its susceptibility to drought, as detected by reduced needle elongation and an association of bark beetle attack with lower needle elongation (a proxy for tree drought stress) in that year, belies its vulnerability. *P. lambertiana* exhibited the least variability in key ecophysiological traits, but this may be due to prior strong, selective pressure by pine blister rust experienced California-wide in the mid 1970's to the mid 1980's. *P. ponderosa* has experienced increased mortality at its southern limit in the Peninsular Range due to drought and outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and western pine beetle (*Dendroctonus brevicomis* LeConte) (40–80% mortality; Grulke et al., 2009) at the western end of the San Bernardino Mountains (L34W). Syncopated stressors, such as drought and bark beetle (*P. ponderosa*), and rusts (*P. lambertiana*) may have reduced variability within the remaining populations and their capacity to respond to environmental change.

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