

Leaf-level physiology in four subalpine plants in tephra-impacted forests during drought

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Abstract: Ecological impacts of climate change in the Pacific Northwest may hinge on acclimation to drier summers, highlighting the importance of plant physiological studies in forests. Evaluating dominant forest plant species under old-growth and managed forest conditions is similarly important as timber harvest might change microclimates and alter drought effects on plants. We examined water potential and gas exchange rates of four dominant plant species in understories of subalpine forests of the Pacific Northwest region of the United States during 2015 — a year with drought conditions representative of future climate projections. We examined two conifer species (*Abies amabilis* Douglas ex J. Forbes and *Tsuga heterophylla* (Raf.) Sarg.) and two huckleberry species (*Vaccinium membranaceum* Douglas ex Torr. and *Vaccinium ovalifolium* Sm.) in old-growth and formerly clear-cut forests at two elevations. Contrary to expectations, we found no evidence of hydraulic stress, and there were no significant differences between old-growth and clear-cut stands, consistent with an edaphic buffering effect in this volcanic landscape. Variation in stem elongation rates among years also indicated the lack of a strong drought response in 2015. Water potential, photosynthesis, and stomatal conductance varied among species and among elevations. In combination, our results help constrain expected physiological activity of understory species in subalpine forests and emphasize the importance of the edaphic context (e.g., tephra deposits) in framing expectations for the responses to drought.

Key words: conifer, drought, photosynthesis, stomatal conductance, *Vaccinium*.

Résumé : Les impacts écologiques des changements climatiques dans le Pacific Northwest pourraient reposer sur l'adaptation à des étés plus secs, soulignant l'importance des études sur la physiologie des plantes dans les forêts. L'évaluation des espèces végétales dominantes en forêt dans des conditions de forêt ancienne ou aménagée est également importante étant donné que la récolte de bois pourrait changer les microclimats et modifier les effets de la sécheresse sur les plantes. Nous avons étudié le potentiel hydrique et les taux d'échanges gazeux de quatre espèces végétales dominantes en sous-étage des forêts subalpines du Pacific Northwest, aux États-Unis, en 2015, une année durant laquelle les conditions de sécheresse étaient représentatives de celles qu'on anticipe avec les changements climatiques. Nous avons étudié deux espèces de conifère (*Abies amabilis* Douglas ex J. Forbes et *Tsuga heterophylla* (Raf.) Sarg.) ainsi que deux espèces d'airelle (*Vaccinium membranaceum* Douglas ex Torr. et *Vaccinium ovalifolium* Sm.) dans des forêts anciennes et des forêts issues d'une coupe rase situées à deux altitudes différentes. Contrairement aux attentes, nous n'avons observé aucun signe de stress hydraulique et il n'y avait aucune différence entre les vieux peuplements et les peuplements issus d'une coupe rase, ce qui est consistant avec un effet tampon du sol dans ce paysage volcanique. La variation du taux annuel d'élongation de la tige témoigne aussi de l'absence d'une forte réaction à la sécheresse en 2015. Le potentiel hydrique, la photosynthèse et la conductance stomatique variaient selon l'espèce et l'altitude. Nos résultats combinés contribuent à limiter les attentes face à l'activité physiologique des espèces de sous-bois dans les forêts subalpines et font ressortir l'importance du contexte édaphique (p. ex. les dépôts de tephra) pour encadrer les attentes vis-à-vis les réactions à la sécheresse. [Traduit par la Rédaction]

Mots-clés : conifère, sécheresse, photosynthèse, conductance stomatique, *Vaccinium*.

Introduction

Climate change is expected to influence the physiology and survival of forest plant species in the Pacific Northwest region of the United States (Chmura et al. 2011), where climate change is projected to result in increased temperatures, with more precipitation in cool seasons and less in the summer (Mote and Salathé 2010). These climatic shifts will likely cause less snowpack, earlier snowmelt, increased evapotranspiration in summer, reduced summer soil moisture, and more severe and frequent droughts (Chmura et al. 2011; Dalton et al. 2013; Sproles et al. 2017). The ecological

consequences of rising temperatures and altered precipitation patterns in high-elevation forests of the Pacific Northwest represent an area of active research (Littell et al. 2010; HilleRisLambers et al. 2015; Ford et al. 2016). How different forest plants will respond is poorly understood, and recent data suggest that responses may be more idiosyncratic than predicted by species distribution models (Ettinger et al. 2011; HilleRisLambers et al. 2015; Ford et al. 2016). In particular, physiologic responses of dominant conifers (HilleRisLambers et al. 2015; Ford et al. 2016) and dominant economically important species such as huckleberries

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(*Vaccinium* sp.) are not well understood in the face of climate change (Boulanger-Lapointe et al. 2017; Houston et al. 2018).

Drought decreases water availability in the soil, which can cause substantial damage to and even large-scale mortality of trees in temperate forests (van Mantgem et al. 2009). Reduced soil water can compromise the multifaceted process of water transfer from soil to roots, resulting in stomatal closure, reduced photosynthesis (Sade et al. 2012), and reduced growth during summer drought (Dalton et al. 2013). Tree mortality rates in the Pacific Northwest may increase with climate change because of increasing water deficits, decreasing snowpack, and vulnerability to disease, insects, and wildfires (Breshears et al. 2009). Although high-elevation forests could have enhanced productivity and growth due to reduced snowpack and warmer temperatures (Peterson and Peterson 2001; Adam et al. 2009; Mote and Salathé 2010; Ford et al. 2016), water limitations resulting from reduced quantity and duration of snowpack could outweigh positive effects of longer growing seasons (Elsner et al. 2010; Trujillo et al. 2012). Due to the complex topography and geologic history of the Pacific Northwest, considerable climatic and edaphic variations occur within small geographic areas, making it difficult to anticipate how the region as a whole will be affected by climate change induced droughts (Dalton et al. 2013). Further, the edaphic influences of frequent volcanic eruptions (e.g., tephra — aerially transported volcanic ejecta — deposition) may alter species responses to drought conditions (Chapin and Bliss 1988; Tejedor et al. 2002; Diaz et al. 2005; Pérez 2009; Le Pennec et al. 2012). Record drought years, including the 2015 summer drought studied here, present a good opportunity to examine plant physiological responses under conditions that mimic the predicted future climate. It is also important to evaluate responses of forest species under both managed and unmanaged forest conditions, as removal of overstory tree canopies in clear-cuts could further alter the effects of drought on remaining plants (Aussenac 2000).

At Mount St. Helens, we exploited an unusual opportunity to evaluate dominant plant species in paired old-growth and previously clear-cut (cut in 1979) forest stands during the historic drought year of 2015. In this dry year, we studied water potential and leaf-level gas exchange (photosynthesis, A ; stomatal conductance, g_s) of two conifer species and two deciduous shrub species representing common plants in Cascade Mountain subalpine forests (Washington State, USA). Water potential was used as an indicator of drought sensitivity, recognizing that isohydric versus anisohydric plant water-use strategies exhibit different patterns with regard to water potential thresholds (Yi et al. 2017). We examined how physiological responses were related to the environment by comparing paired old-growth stands with clear-cut stands in two locations at different elevations. We hypothesized that (i) all species would differ in leaf-level physiology, with the conifers having higher water potential and lower rates of leaf-level gas exchange than the deciduous shrubs and the more forest-associated shrub (*Vaccinium ovalifolium* Sm.; Tappeiner and Alaback 1989) showing greater drought stress than the wider ranging *Vaccinium membranaceum* Douglas ex Torr. (Hamilton and Yearsley 1988); (ii) plants in clear-cut stands would exhibit more negative water potentials compared with plants growing in old-growth stands due to their greater exposure to heat and direct sunlight (Aussenac 2000); and (iii) stands with a history of greater snowpack (higher elevation stands) would show greater drought stress responses. We expected that performance of all species would correlate with measures of soil moisture, leaf temperature, and, in the case of a set of measurements for stem growth, annual values of climatic variables. Because all four species are dominant in high-elevation forests of the Cascade Mountains, we expected that trends in water stress and physiology among species and stands could be indicative of future trends in vegetation associated with climate change.

Methods

Study area and species

This study was conducted during the summer of 2015 in western Washington State, USA, in subalpine old-growth forests and adjacent young stands regenerating on clear-cut sites located approximately 22 km northeast of Mount St. Helens. We sampled these paired old-growth (46.306367N, 121.941027W, and 46.297089N, 121.948005W) and young stands (hereafter referred to as “clear-cut stands”; 46.304907N, 121.937612W, and 46.297581N, 121.952068W) at each of two elevations within the study area (ca. 1160 m and ca. 1256 m, respectively). All stands were within the mid-elevation *Abies amabilis* vegetation zone (Franklin and Dyrness 1988). The two old-growth stands have been used for long-term studies of tephra effects on forest understories (Antos and Zobel 2005; Zobel and Antos 1997, 2017, 2018). Both stands are ca. 600 years old with mostly closed canopies of *Tsuga heterophylla* (Raf.) Sarg., *Tsuga mertensiana* (Bong.) Carrière, and *Abies amabilis* Douglas ex J. Forbes. Average number of trees per hectare (TPH) was 306 for the low-elevation stand, with an average tree diameter at breast height (DBH) of 55 cm. In the high-elevation stand, TPH was approximately 396, with an average tree DBH of, again, about 55 cm. Trees ranged up to over 250 cm DBH in these structurally complex old forests. Each clear-cut stand was chosen to have topography (relatively flat), aspect, and hydrology similar to those of the paired old-growth stand. The clear-cut stands were cut in 1979 (just before the eruption), while the old-growth stands were left intact (Antos and Zobel 2005). A high proportion of planted *Abies procera* Rehder occurs in the canopy of the clear-cut stands, but otherwise, these stands contain the same tree species as the paired old-growth stands. For the low-elevation clear-cut stand, average TPH was approximately 328, with an average tree DBH of ~18 cm. In the high-elevation clear-cut stand, TPH was 156, with an average tree DBH of ~18.5 cm. Trees ranged up to 40 cm DBH in these relatively open young forests. All stands received similar amounts of tephra deposition (ca. 15 cm, primarily pumice of volcanic ash and lapilli texture; Zobel and Antos 1991a, 1997) in the 1980 eruption of Mount St. Helens. The tephra layer consists of tephra fragments smaller than 0.06 mm (approximately 20%–24%), between 0.06 and 1 mm (46%–49%), and larger than 1 mm (17%–19%) (Zobel and Antos 1991a). Soils for all sites are Pelee series soils (Andisols, Ashy over pumiceous, glassy Typic Vitricryands), reflective of the tephra-based edaphic environment typical of many Cascades volcanoes (Mullineaux 1986). The upper elevation stands are located at the foot of steep slopes, but the lower elevation stands are not. Each site was given an acronym based on elevation and site type: CC-L (lower elevation clear-cut), OG-L (lower elevation old-growth), CC-H (higher elevation clear-cut), and OG-H (higher elevation old-growth). Although the elevation difference between the lower and upper sites is only approximately 100 m, the differences in amount and duration of snowpack are typically considerable. On 18 May 1980 (the date of the eruption of Mount St. Helens), 88% of the upper elevation old-growth sites but only 11% of the lower elevation sites were covered with snowpack (Zobel and Antos 1997). Snowpack at the upper elevation sites often persists into early August, whereas snowpack at the lower elevation sites often melts by early June (D. Zobel, personal communication, 2016). The entire study area has a wet maritime climate with heavy snowfall throughout the winter (Franklin and Dyrness 1988; Western Regional Climate Center, <http://www.wrcc.dri.edu/>, 16 August 2016, date last accessed).

The 2015 summer was marked by severe drought conditions in Washington State (United States Drought Monitor, http://droughtmonitor.unl.edu/data/pdf/20150825/20150825_wa_trd.pdf; Sproles et al. 2017) due to (i) unprecedented high temperatures throughout the 2014–2015 winter (National Climatic Data Center, <http://www.ncdc.noaa.gov/sotc/service/national/statewidetakgrank/201412-201502.gif>, January 2016, date last accessed) that resulted in record low mountain

Table 1. PRISM climate variables for study sites based on 2014–2016 observations (totals and means) and 35-year averages (1980–2015; mean \pm 95% CI).

Month	Precipitation (mm)	T_{mean} ($^{\circ}\text{C}$)	VPD_{min} (kPa)	VPD_{max} (kPa)
2014				
June	80.29	9.6	1.58	8.99
July	41.17	15.9	3.87	20.08
2015				
June	21.9	14.75	3.98	18.51
July	21.2	15.89	4.25	21.37
2016				
June	77.96	11.2	2.55	12.69
July	23.45	12.8	1.82	11.13
35-year average				
June	93.37 \pm 17.1	9.54 \pm 0.57	1.34 \pm 0.86	7.74 \pm 1.93
July	32.5 \pm 08.4	13.67 \pm 0.65	2.33 \pm 1.25	11.87 \pm 2.57

Note: T_{mean} , mean temperature; VPD_{min} , minimum vapor pressure deficit; VPD_{max} , and maximum vapor pressure deficit.

snowpack (USDA Natural Resources Conservation Service, <http://www.wcc.nrcs.usda.gov/gis/snow.html>, January 2016, date last accessed), and (ii) the second driest spring and summer on record for the state (National Climatic Data Center, <https://www.ncdc.noaa.gov/sotc/drought/201513>, January 2016, date last accessed). Accordingly, our stands had much lower snowpack and much higher temperatures than normal. The snow water equivalent (SWE) on 1 April (when snowpack levels are often highest) at the Lone Pine weather station, approximately 3.5 km northwest of our study sites, averaged 95.8 cm for the period 1986–2014 but on 1 April 2015 was only 0.8 cm (1% of average). Previous to 2015, the average annual temperature at Lone Pine was 6.4 $^{\circ}\text{C}$, but for 2015, the annual temperature was 8.9 $^{\circ}\text{C}$ (USDA Natural Resources Conservation Service, <http://www.wcc.nrcs.usda.gov/snow/>, April 2016, date last accessed). We also used climate information based on PRISM (4 km resolution; PRISM Climate Group, <http://www.prism.oregonstate.edu/>, September 2017, date last accessed) to interpolate monthly averages for our four stands from 1980 to 2015. Based on these interpolations, average precipitation, temperature, and maximum and minimum vapor pressure deficit (VPD) for the months of June and July (when our study took place) are presented along with averages for 2014–2016 in Table 1. Because stands were closer together than the 4 km resolution of the data and so nearly identical in PRISM-interpolated values, we present a single set of values based on averages of all stands.

Four common forest plant species were chosen for analysis, including saplings of two conifers, *Abies amabilis* (Pacific silver fir) and *Tsuga heterophylla* (western hemlock), and two deciduous shrubs, *Vaccinium membranaceum* (black huckleberry) and *V. ovalifolium* (oval-leaf huckleberry; Zobel and Antos 1997). The two conifers are dominant canopy trees in the stands but are also common in the understory (Antos and Zobel 2005); both species are very shade tolerant and form large seedling banks in forest understories where they often grow very slowly and can persist for over a century (Antos et al. 2005). Average heights of the individuals sampled for each species were 1.30 m for *A. amabilis*, 1.71 m for *T. heterophylla*, 1.03 m for *V. membranaceum*, and 0.97 m for *V. ovalifolium*.

Tsuga heterophylla occurs where there is substantial humidity and precipitation throughout the growing season and is sensitive to drought; top dieback and sapling death are common in years that are especially dry (Burns and Honkala 1990). *Abies amabilis* thrives in maritime to sub-maritime climates with high precipitation and is commonly found in lower montane to subalpine forests (Franklin and Dyrness 1988). It is commonly associated with *T. heterophylla* but tends to occur at higher elevations and is more cold tolerant (Mori et al. 2008).

The two *Vaccinium* spp. are the most abundant shrubs in the forest understory at the old-growth stands (Antos and Zobel 2005) and are also common in young forests following clearcutting. They were adversely affected by a snow–tephra interaction in the 1980 eruption of Mount St. Helens but had mostly recovered by the time of sampling (Zobel and Antos 2017, 2018). *Vaccinium ovalifolium* is a highly shade-tolerant, dominant understory shrub typically found in *T. heterophylla* forests of the Pacific Northwest (Minore 1972; Tappeiner and Alaback 1989) in both clear-cuts and old-growth stands (Haeussler et al. 1990). *Vaccinium membranaceum* is a dominant understory shrub of subalpine forests in the Pacific Northwest and thrives under moderately dense forest canopies or in clear-cuts (Haeussler et al. 1990). It is shade tolerant (Hamilton and Yearsley 1988) but less so than *V. ovalifolium* (Tappeiner and Alaback 1989) and also tolerates drier environments (Franklin and Dyrness 1988).

Within each stand, five microsites were chosen so that individuals of appropriate size of all four species were in close proximity. Within each microsite, one plant of each species was randomly selected and repeatedly measured throughout the study. In a few cases, a nearby plant of a similar size replaced an original plant that did not have enough foliage to allow the full round of measurements. To investigate the effects of increased drought conditions, two full data sets were collected, the first at the end of June and the second at the end of July, 2015. All stands were sampled during four consecutive days during each sampling period. Weather conditions were clear and sunny on all days during the measurements.

Water potential measurements

Water potential (Ψ) was measured at predawn (Ψ_{PD}) when Ψ is generally at a maximum and at midday (Ψ_{MD}) when it is generally at a minimum. Measurements were conducted on each individual plant from all stands using a Scholander pressure chamber (PMS Instrument Company, Corvallis, Oregon; Scholander et al. 1965). Measurements were taken on two to five replicate twigs from each plant until measurements agreed within 0.1 MPa. Predawn measurements were taken between 0330 and 0530, and midday measurements were taken between 1100 and 1300. Percent volumetric soil moisture (θ) in surface soils was measured at the same time as midday water potential, using a soil moisture sensor (SM150, Delta-T Devices Ltd., Cambridge, UK) inserted to a depth of 5 cm. Three soil moisture measurements were taken beneath the canopy of each individual plant and averaged. These soil moisture measurements were taken at shallow depths, which may underestimate water availability deeper in the soil, and our results should be interpreted accordingly.

Leaf-level gas exchange measurements

Midday gas exchange measurements were conducted on all individual plants using an infrared gas analyzer (IRGA) with an open-path continuous-flow leaf chamber (ADC model LCPro+, Analytical Development Co. Ltd., Hoddesdon, UK). This set of measurements included net photosynthesis (A), stomatal conductance (g_s), transpiration (E), and leaf temperature ($^{\circ}\text{C}$). Measurements were taken once per minute for 4 min at three standardized light levels (see below). Values from the last two measurements in each 4-min series (taken at 870 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were averaged for each comparison of A and g_s among stands, species, and measurement periods.

Chamber-based measurements of leaf gas exchange depend on knowing the leaf area present in the chamber. Conifer leaf area was determined using ImageJ analysis software (Schneider et al. 2012) on excised leaves cut to dimensions of the IRGA chamber (6.25 cm^2). The leaves of both huckleberry species generally filled the area of the IRGA leaf chamber; thus, 6.25 cm^2 of each leaf was measured per sample. For smaller huckleberry leaves, leaf area within the chamber was sectioned with a razor blade, and actual leaf area was determined as above for conifer species. During June

measurements, ambient CO₂ was ~394 ppm, midday ambient air temperature was ~27 °C, and midday relative humidity averaged 12.5%. During July measurements, ambient CO₂ was ~394 ppm, midday ambient air temperature was ~30 °C, and midday relative humidity averaged 11.1%.

A red–blue LED array affixed to the leaf chamber was used to manipulate light intensity at three light levels (photosynthetic photon flux density = 80, 470, and 870 μmol photons·m⁻²·s⁻¹). These light levels were chosen to simulate variation from shade to full sun. To compare light saturation points among species, we plotted average photosynthetic rates as a function of three different photosynthetic photon flux densities (PPFD) and fitted a light response curve for each species using linear regression. Briefly, we fit a standardized Michaelis–Menten reaction curve to plots of photosynthesis predicted by PPFD. The general form of the fitted equation for each species was

$$\text{Photosynthetic rate} = \frac{a \times \text{PPFD}}{b + \text{PPFD}}$$

where *a* represents the maximum photosynthetic reaction rate and *b* represents the inverse affinity (a constant). This analysis was conducted primarily to determine the relative light sensitivity of each species. Models were fitted in the nonlinear curve-fit option using the Michaelis–Menten model (2P) in SAS JMP (version JMP Pro 12.0, SAS Institute Inc., Cary, North Carolina, USA).

Canopy coverage and light intensity

In April of 2016, percent canopy coverage was measured at each site using a convex spherical crown densiometer (Forestry Suppliers, Inc., Jackson, Mississippi, USA), and light intensity levels were measured using HOBO Pendant temperature/light 8k data loggers (Onset Computer Co., Bourne, Massachusetts, USA) to investigate site differences in the evergreen conifer canopy cover and light availability that could affect water potential and gas exchange rates. Five densiometer measurements were taken within each microsite and averaged for estimates of canopy cover. Data loggers could detect wavelengths between approximately 200–1200 nm, and weather conditions were clear on the day that measurements were taken. Data loggers were affixed to 1 m PVC poles and light intensity measurements were taken simultaneously at all sites. Data loggers were set to record one reading every 30 s for 7 min, starting at 1200 (noon). Individual measurements within each microsite were averaged for analysis. These data were collected only to clarify obvious differences among stands and should be interpreted cautiously due to the obvious temporal limitations inherent to the measurements.

Stem elongation

While our measurements above provided mechanistic data on physiological responses within the 2015 season, we used measurements of stem elongation on all species to examine longer term presence or absence of stand type and elevation effects and drought responses following the 2015 drought. Shoot elongation can be responsive to both current- and previous-year climate due to bud formation responses to previous climate conditions and current-year sensitivity to climate (Larcher 2003; Seidling et al. 2012). Accordingly, we interpret stem growth responses following and during 2015 as integrative of both drought and nondrought conditions. In late July of 2017, we measured our original study plants (all species) for stem elongation. On each plant that we sampled in 2015, a healthy, uncut, sun-exposed branch was chosen, and stem elongation was measured between clearly defined bud scars for the years 2016, 2015, and 2014. For more detailed analysis through time of a single species, we were able to use *A. amabilis* because extension growth is easily determined from bud scars and growth can be traced for multiple years (King 1997). Needle length in this species can also be measured as an indica-

tion of growth conditions during the growing season. Accordingly, growth measured over several years can be evaluated relative to climate. In 2017, we also measured stem elongation and needle length in *A. amabilis* between 2012 and 2016 on 10 randomly selected individuals in the stand where the most negative water potential measurements were recorded in 2015 (the higher elevation clear-cut site). These data were then evaluated against PRISM-based estimates of average annual precipitation (PPT), temperature, and minimum and maximum VPD (4 km resolution; PRISM Climate Group, <http://www.prism.oregonstate.edu/>, September 2017, date last accessed).

Statistical analysis

We used a repeated-measures linear mixed-effects model design to determine the influence of date, forest type, elevation, and species on each physiological variable (*A*, *g_s*, Ψ_{MD} , Ψ_{PD}). In this restricted maximum likelihood (REML) method approach, maximum likelihood was used to estimate model variance components, which were used to estimate the model effects. In all models, date, site elevation, forest type, and species were fixed effects, while individuals chosen for repeated measures, microsite nested within stand, surface soil moisture, and leaf temperature were random effects. As only two levels of each factor were present for date, elevation, and forest type, significant results indicated differences among levels. In the case of comparison of species, Student's *t* tests were used to determine pairwise differences for all significant effects. Predawn and midday water potentials were analyzed as separate effects. Interaction effects of species × forest type and species × elevation were included in all initial models to determine if individual species responded differently to site variables. When interaction effects were nonsignificant (*p* > 0.05), models were re-run without interactions. Statistical comparisons of *g_s* and *A* values were conducted using average values at high light (photosynthetic photon flux density = 870 μmol photons·m⁻²·s⁻¹). The dependent variables *A*, *g_s*, surface soil moisture, and Ψ_{PD} were not normally distributed (goodness of fit *p* < 0.05) and therefore were either square root transformed (*A*, surface soil moisture, and Ψ_{PD}) or natural log transformed (*g_s*) to achieve normality. Post hoc relationships between the above-mentioned variables and the other environmental variables were explored using Pearson's correlation analysis.

For analysis of stem increment data, a REML approach similar to above was initially used but with the purpose of evaluating differences among years, and these models were run separately for each species because stem elongation data are less meaningful compared across species due to differences in growth form. Year, site elevation, and forest type were used as fixed effects, while individuals chosen for repeated measures and microsite nested within each stand were treated as random effects. A Tukey HSD test was conducted for any significant factors in each model to determine pairwise differences. For stem elongation in *A. amabilis* (where growth was measured between 2012 and 2016), simple linear regression was used to determine strength of prediction of climate variables with stem elongation and needle length through time. We also performed an identical analysis against lagged data in which each year was regressed against the previous year's climate data.

For all analyses, significance was determined based on *p* values < 0.05. All statistical analyses were conducted in SAS JMP (version JMP Pro 12.0, SAS Institute Inc.). Error values presented in the text following means represent one standard error (SE).

Results

Sampling dates

Leaf physiological status changed during the season, with significant differences between dates. Photosynthesis was greater later in the season (*A* (June) = 3.88 ± 0.25 μmol·m⁻²·s⁻¹, *A* (July) =

$4.38 \pm 0.31 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $p = 0.002$), while stomatal conductance was not different between June and July sampling ($p = 0.077$). In July, predawn water potentials were predictably more negative (Ψ_{PD} (June) = -0.477 ± 0.12 MPa, Ψ_{PD} (July) = -0.56 ± 0.25 MPa; $p = 0.013$), but midday water potentials did not differ between dates ($p = 0.240$).

Differences among species

Gas exchange measurements differed significantly among species (Fig. 1). Photosynthetic rates were higher for *V. membranaceum* ($6.80 \pm 0.424 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and *V. ovalifolium* ($4.96 \pm 0.333 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) than for either *T. heterophylla* ($2.79 \pm 0.270 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) or *A. amabilis* ($2.72 \pm 0.297 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $p < 0.05$). *Vaccinium membranaceum* and *V. ovalifolium* also maintained higher average rates of stomatal conductance ($0.12 \pm 0.011 \text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $0.10 \pm 0.008 \text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively) than either *T. heterophylla* ($0.04 \pm 0.004 \text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) or *A. amabilis* ($0.03 \pm 0.003 \text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $p < 0.05$). *Vaccinium ovalifolium* had lower A and g_s than *V. membranaceum* (Fig. 1). Light response curves indicated that both conifers had lower light saturation points than either huckleberry species, and *V. ovalifolium* had a lower light saturation point than *V. membranaceum* (Fig. 2).

At the higher elevation sites, *V. ovalifolium* had lower Ψ_{PD} than any other species, and *T. heterophylla* was lower in Ψ_{PD} than *V. membranaceum* and *A. amabilis* (Fig. 1; Table 2). Both *V. ovalifolium* and *V. membranaceum* had significantly lower Ψ_{MD} than *T. heterophylla* or *A. amabilis* at the same higher elevation sites. At the lower elevation sites, Ψ_{PD} was similar among species, but *V. ovalifolium* had lower Ψ_{MD} than all other species.

Correlations between leaf-level gas exchange and water potential also differed among species but generally suggested few relationships (Table 3). Photosynthesis increased with less negative Ψ_{PD} values only for *T. heterophylla*. For the other species, this correlation was not significant. We also found no significant correlations between A and Ψ_{MD} or between g_s and Ψ_{MD} for any of the species. There was a negative correlation between Ψ_{MD} and Ψ_{PD} for all species. We also found positive correlations for all species between A and g_s .

Photosynthesis (A) and g_s were negatively correlated with average leaf temperature for two species: *V. ovalifolium* and *T. heterophylla*. Nevertheless, in our REML model, leaf temperature rarely accounted for a large proportion of variation in the data (Table 2). We also found no significant correlations for any species between plant height (a proxy for both size and age in our system) and water potential or gas exchange measurements ($p \gg 0.05$; data not shown).

Surface soil moisture (% volumetric) was positively related to g_s in two species, *T. heterophylla* and *V. ovalifolium*. In *V. ovalifolium* only, there was a negative correlation between surface soil moisture and Ψ_{MD} , but there was no relationship with Ψ_{PD} , nor were there relationships between Ψ_{MD} and Ψ_{PD} with other variables in any other species. To further examine differences among species and stands in soil moisture, we used a REML model including repeated measures and microsites nested within stands as random effects and species, forest type, and elevation as fixed effects. In the model, average surface soil moisture was not significantly different among species or elevations, but percent volumetric moisture values were generally low at all stands (OG-L = $10.64\% \pm 0.62\%$, CC-L = $9.93\% \pm 0.59\%$, OG-H = $7.97\% \pm 0.62\%$, and CC-H = $6.66\% \pm 0.49\%$).

Forest type and elevation

There were no significant differences in either photosynthesis (A) or stomatal conductance (g_s) between old-growth and clear-cut sites (A , $p = 0.660$; g_s , $p = 0.148$). Likewise, Ψ_{PD} and Ψ_{MD} were not different between old-growth and clear-cut sites (Ψ_{PD} , $p = 0.978$; Ψ_{MD} , $p = 0.658$; Fig. 1). Photosynthesis (A) was also not significantly different between elevations, although average photosynthetic rates (A) were generally higher in low-elevation stands (Fig. 1; Table 2). Rates of stomatal conductance were $2\times$ greater at low-

elevation sites (average $0.10 \pm 0.008 \text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $p = 0.022$) than at high-elevation sites (average $0.05 \pm 0.004 \text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). For the response variables Ψ_{MD} and Ψ_{PD} , there were significant differences among elevations and interactions between species and elevation (Fig. 1; Table 2). On average, across species and sampling dates, Ψ_{PD} was less negative in lower elevation stands ($p = 0.021$; average -0.47 ± 0.02 MPa) than in higher elevation stands (average -0.56 ± 0.02 MPa), and Ψ_{MD} was significantly more negative in the higher elevation stands ($p < 0.001$), though this was only observable after accounting for date and species. Interestingly, in a similar REML model using leaf temperature as the response variable, leaf temperature was significantly lower at the lower elevation stands (average $25.29 \pm 0.57^\circ\text{C}$ to $24.72 \pm 0.42^\circ\text{C}$) than at either high-elevation stand (average $32.64 \pm 0.48^\circ\text{C}$ to $30.46 \pm 0.33^\circ\text{C}$; $p < 0.05$). Average leaf temperature was significantly higher at the high-elevation clear-cut stand, CC-H, than at the high-elevation old-growth stand, OG-H ($p < 0.05$).

Canopy coverage and light intensity

No significant correlations were found between percent canopy cover or light intensity levels and any other measurement (Ψ_{PD} , Ψ_{MD} , A , g_s , leaf temperature, or percent soil moisture; $p \gg 0.05$). Percent canopy cover was highest at the high-elevation old-growth stand (averaging $83.2\% \pm 2.7\%$ coverage) and lowest at the high-elevation clear-cut stand (averaging $7.0\% \pm 1.9\%$ coverage), while the lower elevation stands had intermediate values, with the old-growth stand averaging $69.4\% \pm 5.9\%$ coverage and the clear-cut stand averaging $53.6\% \pm 4.5\%$ coverage, reflecting tree regrowth of the stand since the initial clear-cut (in 1979). Our brief measures of light intensity levels mirrored canopy coverage. Average light intensity ($\pm\text{SE}$) was lowest at the high-elevation old-growth stand ($4\ 847 \pm 615 \text{lumens (lm)}\cdot\text{m}^{-2}$), highest at the high-elevation clear-cut stand ($91\ 953 \pm 25\ 531 \text{lm}\cdot\text{m}^{-2}$), and intermediate at the low-elevation old-growth stand ($14\ 127 \pm 4\ 156 \text{lm}\cdot\text{m}^{-2}$) and the adjacent low-elevation clear-cut stand ($15\ 537 \pm 2\ 224 \text{lm}\cdot\text{m}^{-2}$).

Stem elongation

There was no significant difference in stem elongation between 2014, 2015, and 2016 for *A. amabilis*, *V. membranaceum*, or *V. ovalifolium* despite clear differences in growing-season conditions between years in precipitation, temperature, and VPD (Table 1). Elevation and forest type were also nonsignificant ($p > 0.05$). Average stem elongation (cm, $\pm\text{SE}$) for these species in order of year (2014, 2015, 2016) was 7.47 ± 0.65 , 7.07 ± 0.59 , and 6.3 ± 0.59 for *A. amabilis*, 9.4 ± 2.33 , 10.7 ± 1.05 , and 10.01 ± 1.02 for *V. ovalifolium*, and 6.47 ± 2.22 , 8.7 ± 1.06 , and 8.64 ± 1.06 for *V. membranaceum*. For *T. heterophylla*, stem elongation in 2014 (10.74 ± 1.0 cm) was significantly greater than 2016 stem elongation (7.98 ± 0.91 cm; $p < 0.05$), while 2015 was not significantly different from the other years (9.6 ± 0.91 cm).

For *A. amabilis* measured between 2012 and 2016, stem elongation was uncorrelated with annual or June and July variation in precipitation, average temperature, or maximum or minimum VPD ($p > 0.05$). Needle length, however, was significantly related to both maximum VPD ($r^2 = 0.81$, $p = 0.025$) and minimum VPD ($r^2 = 0.73$, $p = 0.040$) but differed in the opposite direction than was hypothesized; needle length did not decrease, but instead increased with higher VPD values. When data were lagged to regress stem increment and needle length against previous year's data, there were no significant relationships ($p > 0.05$).

Discussion

We identified significant differences in water potential and function associated with species and elevation. *Vaccinium ovalifolium* and *T. heterophylla* had significantly lower Ψ_{PD} than *V. membranaceum* and *A. amabilis* at the higher elevation sites. We found significantly lower rates of photosynthesis and stomatal conductance in the conifer than in the deciduous huckleberry species (Figs. 1 and 2). These

Fig. 1. Leaf gas exchange and water potential measurements of four species (*Abies amabilis* (ABAM), *Tsuga heterophylla* (TSHE), *Vaccinium membranaceum* (VAME), and *Vaccinium ovalifolium* (VAOV)) at two pairs of forest stand types (clear-cut (CC) and old growth (OG)) and two elevations (high elevation (H) and low elevation (L)). Points on each graph represent means for groups, and error bars represent ± 1 SE. For photosynthesis (A) and stomatal conductance (g_s), interactions between species and elevation or forest type were not significant, so means for each factor (species, forest type, and elevation) are presented separately. For predawn (Ψ_{PD}) and midday (Ψ_{MD}) water potential, interactions between species and elevation were significant, so these data are displayed in the same graph, with open circles representing least square means for high-elevation stands and solid circles representing least square means for low-elevation stands (± 1 SE). Different lowercase letters denote significant differences based on Student's *t* tests. ns, not significant.

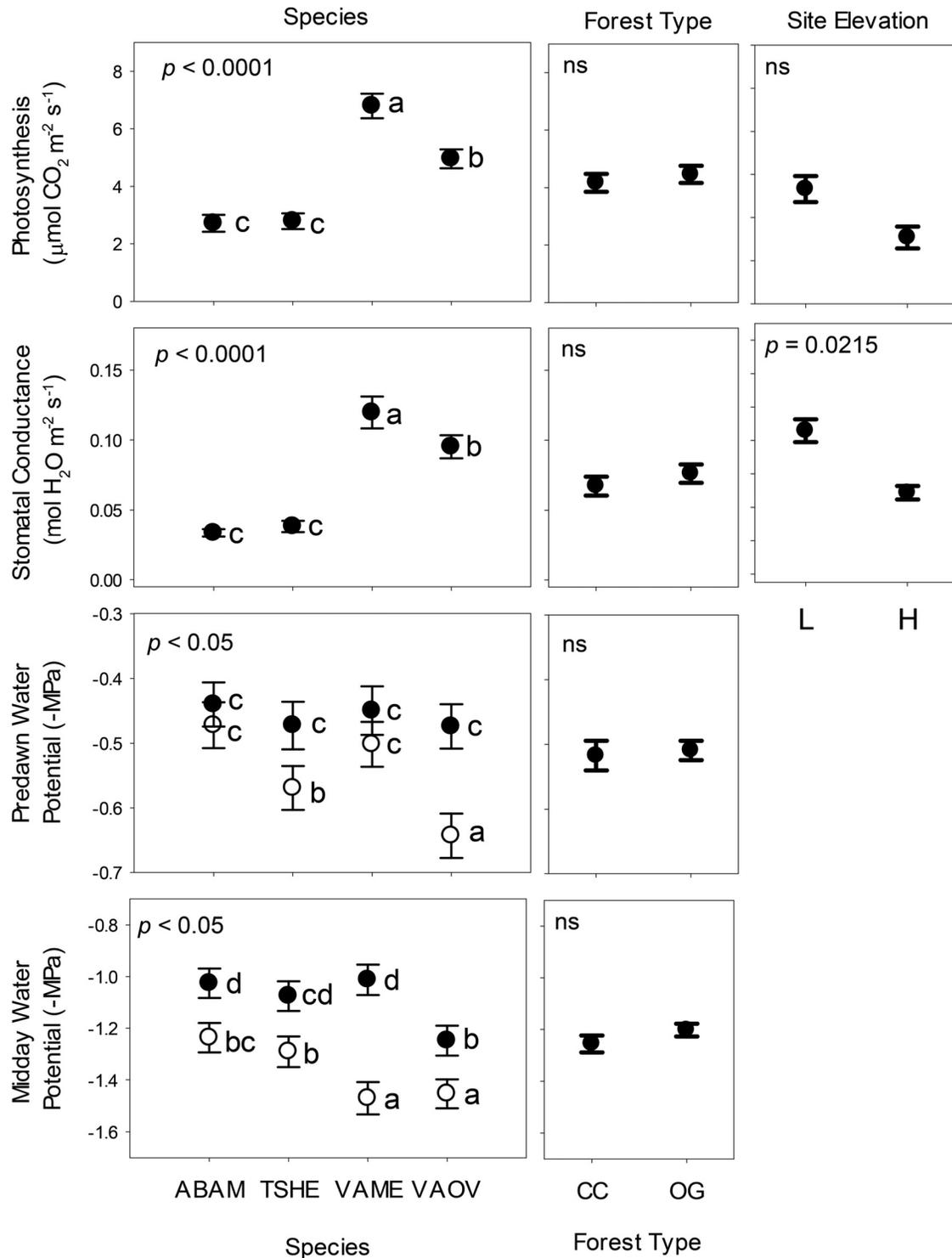
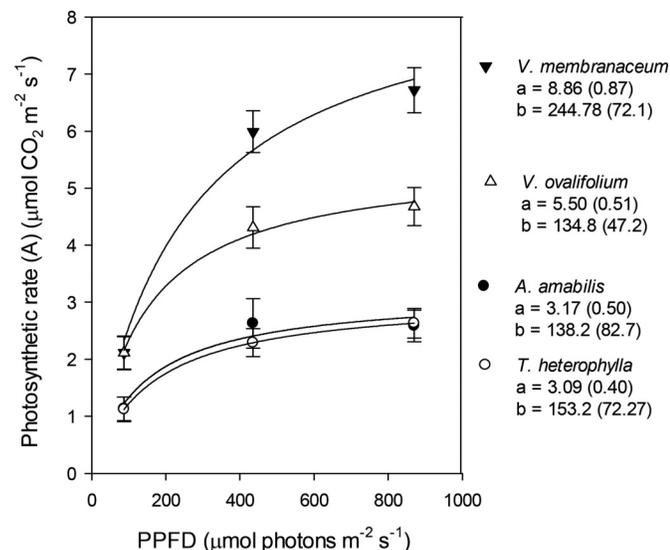


Fig. 2. Rates of leaf net photosynthesis in response to photosynthetic photon flux density (PPFD) of four species: *Tsuga heterophylla* (○), *Abies amabilis* (●), *Vaccinium ovalifolium* (△), and *Vaccinium membranaceum* (▼). Points on the graph represent means, and error bars represent ± 1 SE. Values after the name of each species represent least squares parameter (*a* and *b*) estimates for each model, with ± 1 SE in parentheses. All models were significant at $p < 0.001$, with R^2 estimates > 0.9 .



results are consistent with lower gas exchange in the conifer species resulting in lower water stress and consistent with more conservative water relations overall in conifers. Similarly, in comparison with conifer species at high elevation, Ψ_{MD} was lower for both *Vaccinium* species. We also found that the light response curves (Fig. 2) suggested lower light saturation points for both *A. amabilis* and *T. heterophylla* than for either *Vaccinium* species, consistent with our hypothesis that leaf-level gas-exchange rates would be higher in the deciduous huckleberries than in the evergreen conifers. While comparisons among these species groups were often significant, they are also generally in agreement with well-established differences between conifer and deciduous species (Marshall and Waring 1984). Accordingly, we next discuss sequential results for conifers and *Vaccinium* species separately before returning to our overall hypotheses and general patterns.

Two conifers

Although both *T. heterophylla* and *A. amabilis* are highly shade tolerant and occur in mild, wet climates (Burns and Honkala 1990), *A. amabilis* tends to be more cold tolerant (Mori et al. 2008), with deeper root systems (as discussed above; Zobel and Antos 1991b). Such cold tolerance could be correlated with higher drought tolerance due to similarities in freezing and drought on stem embolisms (Siminovitch and Cloutier 1983; Blödner et al. 2005). Our results suggested similar photosynthetic rates and stomatal conductance between *A. amabilis* and *T. heterophylla* but differences in predawn and midday water potential at a higher elevation stand where *T. heterophylla* had significantly lower Ψ_{PD} than *A. amabilis*. The latter species may have deeper or more extensive root systems relative to leaf area, which allows access to deeper, wetter soil layers and more rapid overnight recovery of water potential. Mature *T. heterophylla* have a relatively shallow root system (Eis 1987), and *A. amabilis* seedlings have deeper and more complex roots, as well as a higher tolerance for shade and limited soil moisture, than *T. heterophylla* seedlings (Zobel and Antos 1991b). The two conifer species were well matched in their light response curves, suggesting similar shade tolerance.

Comparison of our data with previous studies that measured similar species under water stress clearly demonstrates that we observed water potential values for conifers far from threshold values that initiate damage to plant processes, e.g., minimum xylem water potentials > -2 MPa are rarely associated with greater than 50% loss of function in conifers (Choat et al. 2012). Although *T. heterophylla* is sensitive to drought in comparison with other species (e.g., Bond and Kavanagh 1999), Kavanagh and Zaerr (1997) found that *T. heterophylla* showed little loss of hydraulic conductivity at xylem pressure potentials > -2.0 MPa, and below -2.1 MPa, conductance may decline with decreasing water potential (Bond and Kavanagh 1999). Embolisms in *T. heterophylla* are known to rapidly escalate below -2.5 to -2.8 MPa, with complete cavitation occurring at -4.0 MPa (Kavanagh and Zaerr 1997). In comparison, we obtained an average midday water potential of -1.18 MPa for *T. heterophylla* and found no indication of stomatal closure in response to stress. Our results for *A. amabilis* were similar. In a review of embolism thresholds for 40 species in the Pinaceae, Martínez-Vilalta et al. (2004) reported that for eight species of *Abies*, 50% of conductivity was lost at an average water potential of -3.4 MPa and ranged from -2.75 (*A. balsamea*) to -4.0 MPa (*A. concolor*). In a recent global review of vulnerability to drought in more than 226 species worldwide (Choat et al. 2012), the minimum xylem tensions in the field for gymnosperms generally averaged lower than -2.0 MPa, and the point at which greater than 50% of xylem conductivity was lost was often lower than -2.5 MPa. In comparison, *A. amabilis* in our study had average midday water potential values of only -1.14 MPa. Conifers may operate within a water potential range that grants a wide safety margin from drought-induced embolisms (Choat et al. 2012). Even so, under drought conditions, we expected to see values that were more consistent with the known thresholds in water potential for conifers. Stomatal conductance measurements at midday for *T. heterophylla* and *A. amabilis* were low enough to be consistent with values indicating stomatal closure in responses to high leaf-to-air vapor pressure gradients (Bond and Kavanagh 1999), but positive photosynthesis values indicated that low stomatal conductance was not occurring at the expense of carbon gain. Similarly, stem elongation data suggested no declines in growth, while needle lengths increased with VPD for *A. amabilis*. These results may be consistent with a study examining *T. mertensiana* in the Washington Cascades where growth was negatively correlated with spring snowpack and positively associated with hotter, drier summers (Peterson and Peterson 2001).

Two huckleberry species

We observed differences in gas exchange between the two huckleberries. The more shade-tolerant *V. ovalifolium* (Hamilton and Yearsley 1988; Alaback and Tappeiner 1991) showed lower photosynthesis and stomatal conductance and a lower light saturation point than *V. membranaceum*. Both species exhibited rates of photosynthesis and stomatal conductance that were approximately 2–3 times higher than those of neighboring conifers. In addition to a higher gas exchange rate, *V. membranaceum* had less negative water potentials than *V. ovalifolium*. *Vaccinium membranaceum* tends to tolerate warmer, drier habitats than *V. ovalifolium* (Franklin and Dyrness 1988), which could be consistent with deeper roots. The difference in water potential between the *Vaccinium* species could be associated with higher preference for shade and moisture in *V. ovalifolium* than in *V. membranaceum* (Franklin and Dyrness 1988; Haussler et al. 1990), which resulted in lower water potential.

In a global analysis of the drivers of drought tolerance across more than 377 species, xylem water potential values indicative of drought were rarely as high as the midday water potential values that we found for *Vaccinium* (Bartlett et al. 2012). Our measured values were again generally above thresholds associated with water

Table 2. Results of REML model for response variables photosynthesis and stomatal conductance (A and g_s , respectively, at 870 PAR) and midday and predawn xylem water potential (Ψ_{MD} and Ψ_{PD} , respectively).

	df (num/den)	F	p	R^2_{adj}	Random effect	% of total
A at 870 PAR						
Date	1/78.32	9.8936	0.0023	0.5830	Repeated measure	0.195
Elevation	1/36.62	0.4251	0.5185		Microsite[stand]	8.255
Forest type	1/17.88	0.2005	0.6597		Soil moisture (% volume)	0.058
Species	3/57.38	44.3322	<0.0001		Leaf temperature	0.895
g_s at 870 PAR						
Date	1/79.72	3.2210	0.0765	0.4210	Repeated measure	0.000
Elevation	1/12.64	6.8808	0.0215		Microsite[stand]	5.499
Forest type	1/16.62	2.2981	0.1483		Leaf temperature	0.229
Species	3/55.06	96.112	<0.0001		Soil moisture (% volume)	0.008
Ψ_{MD}						
Date	1/75.73	1.4028	0.2400	0.3917	Repeated measure	0.000
Elevation	1/42.74	13.1427	0.0008		Microsite[stand]	15.503
Forest type	1/17.63	0.2028	0.6579		Leaf temperature	2.590
Species	3/50.66	9.0011	<0.0001		Soil moisture (% volume)	0.271
Elevation \times species	3/49.82	3.6807	0.0180			
Ψ_{PD}						
Date	1/79	6.4273	0.0132	-0.2974	Repeated measure	0.000
Elevation	1/17	6.4469	0.0212		Microsite[stand]	16.052
Forest type	1/17	0.0008	0.9782			
Species	3/54	7.7455	0.0002			
Elevation \times species	3/54	3.0595	0.0359			

Note: Significant p values are indicated in bold. df, degrees of freedom (numerator (num), denominator (den)).

Table 3. Correlations, with p values in parentheses, between physiological measures and abiotic variables.

Variable	A	g_s	Ψ_{PD}	Ψ_{MD}	Leaf temperature ($^{\circ}C$)	θ (% volume)
A. amabilis						
A	1	0.4636 (0.0026)	0.2248 (0.1632)	-0.0921 (0.572)	-0.263 (0.1157)	0.2915 (0.068)
g_s		1	0.2228 (0.1669)	-0.0521 (0.7496)	-0.234 (0.1634)	0.046 (0.7779)
Ψ_{PD}			1	-0.2628 (0.1013)	0.0986 (0.5616)	-0.0278 (0.865)
Ψ_{MD}				1	0.2832 (0.0894)	-0.1361 (0.4024)
Leaf temperature ($^{\circ}C$)					1	-0.2524 (0.1318)
θ (% volume)						1
T. heterophylla						
A	1	0.7663 (<0.0001)	0.4415 (0.0043)	0.0884 (0.5874)	-0.4780 (0.0032)	0.1117 (0.4925)
g_s		1	0.2366 (0.1416)	0.0552 (0.735)	-0.5106 (0.0015)	0.3558 (0.0243)
Ψ_{PD}			1	-0.3374 (0.0332)	0.2254 (0.1863)	0.0345 (0.8327)
Ψ_{MD}				1	0.2638 (0.1201)	-0.2608 (0.104)
Leaf temperature ($^{\circ}C$)					1	-0.1839 (0.283)
θ (% volume)						1
V. membranaceum						
A	1	0.8293 (<0.0001)	0.1503 (0.3548)	-0.1848 (0.2535)	-0.4309 (0.011)	0.3346 (0.0348)
g_s		1	0.0812 (0.6185)	-0.2208 (0.171)	-0.4604 (0.0061)	0.3878 (0.0134)
Ψ_{PD}			1	-0.3532 (0.0254)	0.3632 (0.0347)	-0.2763 (0.0844)
Ψ_{MD}				1	0.0368 (0.8362)	-0.1254 (0.4408)
Leaf temperature ($^{\circ}C$)					1	-0.4998 (0.0026)
θ (% volume)						1
V. ovalifolium						
A	1	0.5293 (0.0004)	0.2379 (0.1394)	0.1028 (0.5277)	-0.3687 (0.0227)	0.193 (0.2328)
g_s		1	0.2557 (0.1113)	0.1695 (0.2957)	-0.5916 (<0.0001)	0.3403 (0.0317)
Ψ_{PD}			1	-0.4353 (0.005)	0.2517 (0.1274)	-0.241 (0.1341)
Ψ_{MD}				1	0.3739 (0.0208)	-0.4246 (0.0063)
Leaf temperature ($^{\circ}C$)					1	-0.2734 (0.0967)
θ (% volume)						1

Note: Significant correlations are in bold. A, photosynthesis; g_s , stomatal conductance; Ψ_{MD} , midday xylem water potential; Ψ_{PD} , predawn xylem water potential; θ , volumetric soil moisture.

stress that reduces rates of gas exchange. While the species that we studied have not been evaluated for water stress thresholds, many studies of boreal and commercial *Vaccinium* exist. In boreal species, the 88% conductivity loss thresholds for water potential were -3.31 MPa (*V. myrtillus*) and -3.15 MPa (*V. vitis-idaea*; Ganthaler and Mayr 2015). In commercial blueberry (*V. corymbosum*), stomatal

conductance and photosynthesis declined under the “moderate” stress, at -1.94 MPa (Rho et al. 2012). In comparison, the average midday water potential of the plants in our study were -1.23 MPa (*V. membranaceum*) and -1.36 MPa (*V. ovalifolium*), with minimal values of -1.9 and -1.83 MPa, respectively. Thus, even without a clear control group, these data cumulatively suggest an absence of

threshold water potential levels in our data, even in a historic drought year.

Stand differences

We observed a consistent difference in that plants in higher elevation stands had significantly lower levels of stomatal conductance and water potential but higher average leaf temperatures than plants growing at the lower elevation stands. What would cause plants growing at a higher elevation to have higher water stress and lower leaf-level gas exchange? Differences in canopy cover could be one explanation if canopy cover was greater at the lower elevation than at the higher elevation old-growth stand, as an increase in direct sunlight and heat could reduce water potential and gas exchange rates as plants closed their stomata (Aussenac 2000). Nevertheless, our data showed a significantly denser canopy at the higher elevation than at the lower elevation old-growth stand and showed no significant correlations between canopy cover and water potential or gas exchange measurements. Additionally, in our comparisons between clear-cut and old-growth forests, which differ in canopy cover due to management history, we found virtually no significant differences in water potential or leaf-level physiology at either elevation. Thus, canopy cover does not appear to be a notable contributing factor to the physiological differences between plants growing at the two different elevations. We speculate that differences with elevation could be related to effects of record low snowpack levels in 2014–2015 (USDA Natural Resources Conservation Service, <http://www.wcc.nrcs.usda.gov/snow/snotel-wedata.html>, January 2016, date last accessed), where plants in higher elevation stands with historically greater snowpack (Antos and Zobel 2005) might not be as well acclimated to absence of summer snowmelt during drier conditions (Hu et al. 2010; Trujillo et al. 2012). Nevertheless, this hypothesis is speculative only.

We had expected that clear-cut stands would show greater water stress, resulting in lower leaf-level photosynthesis and stomatal conductance rates; we found no such significant differences. Previous studies have found that plants growing in young-growth stands generally have lower water potentials than those growing under a forest canopy due to greater heat, direct sunlight, and competition from herbaceous vegetation (Aussenac 2000). Four main hypotheses might explain the lack of differences between stand types in our study: (i) species growing in clear-cuts have acclimated to drier conditions; (ii) low precipitation interception in a clear-cut results in more water reaching the roots (Berris and Harr 1987); (iii) lower ecosystem-level leaf area results in lower transpiration demand on available water (Vertessy et al. 1995); and (iv) high water-holding capacity of pumice soils and a mulching effect of the 1980 tephra may have increased available water. These explanations are not mutually exclusive and may all contribute to our results. Nevertheless, multiple lines of evidence suggest that realized drought may have been less than anticipated in both clear-cut and old-growth environments.

Drought year?

Overall, we found less water stress in response to drought than we had expected during the historic drought year of 2015. In comparison with the past 35 years, our sites received 25%–67% of average precipitation, were 2–5 °C warmer, and had maximum and minimum VPD that was between 1.8 and 3 times greater than average. The following year (2016) was nearly average. While we had no controls for the drought, a comparison of stem elongation rates among years did not demonstrate differences between growth in the drought year and growth in the other year for all species. In fact, the only significant difference among years suggested greater stem elongation rates for *T. heterophylla* in 2014 versus 2016 but no differences in 2015 (the drought year; Table 1). Further, in *A. amabilis*, the significant correlations between needle length and VPD suggested increases in needle length with VPD.

If our results represent the status of understory shrubs and conifer saplings at our sites in 2015, why were these plants not experiencing obvious water stress in the midst of historic drought conditions? One hypothesis is that the soil composed of tephra from previous volcanic eruptions has a high water-holding capacity and insulating effect (Kimsey et al. 2008) that prevented plants from reaching severely low water potential. This hypothesis aligns with previous studies in which pumice-based soils were found to have high water-holding capacity (Zobel 1974; Geist and Cochran 1991; Tejedor et al. 2002) and studies that have found tree species to be sensitive to changes in soil water-holding capacity (Mathys et al. 2014; Lévesque et al. 2016). If true, this finding may be relevant to widespread expectations of severe water stress in western forests with increasing drought. The elevated tree mortality observed in the western United States in relation to climate change and drought (van Mantgem et al. 2009) is likely context dependent and may not become as prevalent in tephra-impacted forests as in areas without recent tephra. Mortality following drought can also be delayed (Berdanier and Clark 2016); thus it would be premature to assume — even though water potential was higher than expected — that there are no long-term effects of the 2015 drought. In any case, our results are consistent with the concept that substrate could strongly modify predicted effects of climate change (Chapin and Bliss 1988; Tejedor et al. 2002; Diaz et al. 2005; Pérez 2009; Le Pennec et al. 2012).

Overall, our results suggest (i) differences among species, including higher rates of photosynthesis and stomatal conductance in dominant understory shrubs compared with conifers, (ii) differences among elevations, (iii) a lack of strong physiological effects from differences in forest structure (old-growth versus young-growth stands), and (iv) a lack of strong drought effects on physiological responses of understory species and conifer saplings during a historic drought year. While not conclusive, our results are potentially consistent with the concept that local edaphic factors may play a role in buffering species-specific physiological responses to the environment. Additionally, species and locale differences may persist in drought years even in the absence of major realized water stress.

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References

- Adam, J.C., Hamlet, A.F., and Lettenmaier, D.P. 2009. Implications of global climate change for snowmelt hydrology in the twenty-first century. *Hydrol. Processes*, 23(7): 962–972. doi:10.1002/hyp.7201.
- Alaback, P.B., and Tappeiner, J.C., II. 1991. Response of western hemlock (*Tsuga heterophylla*) and early huckleberry (*Vaccinium ovalifolium*) seedlings to forest windthrow. *Can. J. For. Res.* 21(4): 534–539. doi:10.1139/x91-074.
- Antos, J.A., and Zobel, D.B. 2005. Plant responses in forests of the tephra-fall zone. In *Ecological responses to the 1980 eruption of Mount St. Helens*. Edited by V.H. Dale, F.J. Swanson, and C.M. Crisafulli. Springer, New York. pp. 47–58. doi:10.1007/0-387-28150-9_4.
- Antos, J.A., Guest, H.J., and Parish, R. 2005. The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat. *J. Ecol.* 93(3): 536–543. doi:10.1111/j.1365-2745.2005.00968.x.
- Aussenac, G. 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Ann. For. Sci.* 57(3): 287–301. doi:10.1051/forest:2000119.
- Bartlett, M.K., Scoffoni, C., and Sack, L. 2012. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global

- meta-analysis. *Ecol. Lett.* **15**(5): 393–405. doi:10.1111/j.1461-0248.2012.01751.x. PMID:22435987.
- Berdanier, A.B., and Clark, J.S. 2016. Multiyear drought-induced morbidity preceding tree death in southeastern U.S. forests. *Ecol. Appl.* **26**(1): 17–23. doi:10.1890/15-0274. PMID:27039506.
- Berris, S.N., and Harr, R.D. 1987. Comparative snow accumulation and melt during rainfall in forested and clear-cut plots in the Western Cascades of Oregon. *Water Resour. Res.* **23**(1): 135–142. doi:10.1029/WR023i001p00135.
- Blödner, C., Skroppa, T., Johnsen, Ø., and Polle, A. 2005. Freezing tolerance in two Norway spruce (*Picea abies* [L.] Karst.) progenies is physiologically correlated with drought tolerance. *J. Plant Physiol.* **162**(5): 549–558. doi:10.1016/j.jplph.2004.09.005. PMID:15940872.
- Bond, B.J., and Kavanagh, K.L. 1999. Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. *Tree Physiol.* **19**(8): 503–510. doi:10.1093/treephys/19.8.503. PMID:12651540.
- Boulanger-Lapointe, N., Järvinen, A., Partanen, R., and Herrmann, T.M. 2017. Climate and herbivore influence on *Vaccinium myrtillus* over the last 40 years in northwest Lapland, Finland. *Ecosphere*, **8**(1): e01654. doi:10.1002/ecs2.1654.
- Breshears, D.D., Myers, O.B., Meyer, C.W., Barnes, F.J., Zou, C.B., Allen, C.D., McDowell, N.G., and Pockman, W.T. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Front. Ecol. Environ.* **7**(4): 185–189. doi:10.1890/080016.
- Burns, R.M., and Honkala, B.H. 1990. *Silvics of North America: Vol. 1: conifers* [online]. USDA Forest Service Agric. Handb. 654. Available from http://www.srs.fs.usda.gov/pubs/misc/ag_654_voll1.pdf [accessed 3 March 2017].
- Chapin, D.M., and Bliss, L.C. 1988. Soil-plant water relations of two subalpine herbs from Mount St. Helens. *Can. J. Bot.* **66**(5): 809–818. doi:10.1139/b88-118.
- Chmura, D.J., Anderson, P.D., Howe, G.T., Harrington, C.A., Halofsky, J.E., Peterson, D.L., Shaw, D.C., and St. Clair, J.B. 2011. Forest responses to climate change in the northwestern United States: ecophysiological foundations for adaptive management. *For. Ecol. Manage.* **261**(7): 1121–1142. doi:10.1016/j.foreco.2010.12.040.
- Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., and Zanne, A.E. 2012. Global convergence in the vulnerability of forests to drought. *Nature*, **491**: 752–755. doi:10.1038/nature11688. PMID:23172141.
- Dalton, M.M., Mote, P.W., and Snover, A.K. 2013. Climate change in the Northwest: implications for our landscapes, waters, and communities. Island Press, Washington, D.C. doi:10.5822/978-1-61091-512-0.
- Diaz, F., Jimenez, C.C., and Tejedor, M. 2005. Influence of the thickness and grain size of tephra mulch on soil water evaporation. *Agric. Water Manage.* **74**(1): 47–55. doi:10.1016/j.agwat.2004.10.011.
- Eis, S. 1987. Root systems of older immature hemlock, cedar, and Douglas-fir. *Can. J. For. Res.* **17**(11): 1348–1354. doi:10.1139/x87-208.
- Elsner, M.M., Cuo, L., Voisin, N., Deems, J.S., Hamlet, A.F., Vano, J.A., Mickelson, K.E.B., Lee, S.Y., and Lettenmaier, D.P. 2010. Implications of 21st century climate change for the hydrology of Washington State. *Clim. Change*, **102**: 225–260. doi:10.1007/s10584-010-9855-0.
- Ettinger, A.K., Ford, K.R., and HilleRisLambers, J. 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology*, **92**(6): 1323–1331. doi:10.1890/10-1639.1. PMID:21797160.
- Ford, K.R., Harrington, C.A., Bansal, S., Gould, P.J., and St. Clair, J.B. 2016. Will changes in phenology track climate change? A study of growth initiation timing in coast Douglas-fir. *Global Change Biol.* **22**(11): 3712–3723. doi:10.1111/gcb.13328.
- Franklin, J.F., and Dyrness, C.T. 1988. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, Ore.
- Ganthalter, A., and Mayr, S. 2015. Dwarf shrub hydraulics: two *Vaccinium* species (*Vaccinium myrtillus*, *Vaccinium vitis-idaea*) of the European Alps compared. *Physiol. Plant.* **155**(4): 424–434. doi:10.1111/ppl.12333. PMID:25677081.
- Geist, J.M., and Cochran, P.H. 1991. Influences of volcanic ash and pumice deposition on productivity of western interior forest soils. In *Proceedings — Management and Productivity of Western-Montane forest soils*, Boise, Idaho, 10–12 April 1990. Edited by A.E. Harvey and L.F. Neuenschwander. USDA Forest Service, Intermountain Research Station, Ogden, Utah. Gen. Tech. Rep. INT-280. pp. 82–88.
- Haeussler, S., Coates, D., and Mather, J. 1990. *Autecology of common plants in British Columbia: a literature review*. British Columbia Ministry of Forests, Research Branch, Victoria, B.C., FRDA Rep. 158.
- Hamilton, E.H., and Yearsley, K.H. 1988. *Vegetation development after clearcutting and site preparation in the SBS zone*. British Columbia Ministry of Forests, Research Branch, Victoria, B.C., FRDA Rep. 018.
- HilleRisLambers, J., Anderegg, L.D.L., Breckheimer, I., Burns, K.M., Ettinger, A.K., Franklin, J.F., Freund, J.A., Ford, K.R., and Kroll, S.J. 2015. Implications of climate change for turnover in forest composition. *Northwest Sci.* **89**(3): 201–218. doi:10.3955/046.089.0304.
- Houston, L., Capalbo, S., Seavert, C., Dalton, M., Bryla, D., and Sagili, R. 2018. Specialty fruit production in the Pacific Northwest: adaptation strategies for a changing climate. *Clim. Change*, **146**(1–2): 159–171. doi:10.1007/s10584-017-1951-y.
- Hu, J., Moore, D.J.P., Burns, S.P., and Monson, R.K. 2010. Longer growing seasons lead to less carbon sequestration by a subalpine forest. *Global Change Biol.* **16**(2): 771–783. doi:10.1111/j.1365-2486.2009.01967.x.
- Kavanagh, K.L., and Zaerr, J.B. 1997. Xylem cavitation and loss of hydraulic conductance in western hemlock following planting. *Tree Physiol.* **17**(1): 59–63. doi:10.1093/treephys/17.1.59. PMID:14759915.
- Kimsey, M.J., Moore, J., and McDaniel, P. 2008. A geographically weighted regression analysis of Douglas-fir site index in north central Idaho. *For. Sci.* **54**(3): 356–366.
- King, D.A. 1997. Branch growth and biomass allocation in *Abies amabilis* saplings in contrasting light environments. *Tree Physiol.* **17**(4): 251–258. doi:10.1093/treephys/17.4.251. PMID:14759864.
- Larcher, W. 2003. *Physiological plant ecology: ecophysiology and stress physiology of functional groups*. Springer-Verlag, Berlin, Heidelberg.
- Lévesque, M., Walthert, L., and Weber, P. 2016. Soil nutrients influence growth response of temperate tree species to drought. *J. Ecol.* **104**(2): 377–387. doi:10.1111/1365-2745.12519.
- Le Penneq, J.-L., Ruiz, G.A., Ramón, P., Palacios, E., Mothes, P., and Yepes, H. 2012. Impact of tephra falls on Andean communities: the influences of eruption size and weather conditions during the 1999–2001 activity of Tungurahua volcano, Ecuador. *J. Volcanol. Geotherm. Res.* **217–218**: 91–103. doi:10.1016/j.jvolgeores.2011.06.011.
- Littell, J.S., Oneil, E.E., McKenzie, D., Hicke, J.A., Lutz, J.A., Norheim, R.A., and Elsner, M.M. 2010. Forest ecosystems, disturbance, and climatic change in Washington State, USA. *Clim. Change*, **102**(1–2): 129–158. doi:10.1007/s10584-010-9858-x.
- Marshall, J.D., and Waring, R.H. 1984. Conifers and broadleaf species: stomatal sensitivity differs in western Oregon. *Can. J. For. Res.* **14**(6): 905–908. doi:10.1139/x84-161.
- Martínez-Vilalta, J., Sala, A., and Piñol, J. 2004. The hydraulic architecture of Pinaceae — a review. *Plant Ecol.* **171**(1–2): 3–13. doi:10.1023/B:VEGE.0000029378.87169.b1.
- Mathys, A., Coops, N.C., and Waring, R.H. 2014. Soil water availability effects on the distribution of 20 tree species in western North America. *For. Ecol. Manage.* **313**: 144–152. doi:10.1016/j.foreco.2013.11.005.
- Minore, D. 1972. *The wild huckleberries of Oregon and Washington — a dwindling resource*. USDA Forest Service, Pacific Northwest Research Station, Portland, Ore., Res. Pap. PNW-RP-143.
- Mori, A.S., Mizumachi, E., and Sprugel, D.G. 2008. Morphological acclimation to understory environments in *Abies amabilis*, a shade- and snow-tolerant conifer species of the Cascade Mountains, Washington, USA. *Tree Physiol.* **28**(5): 815–824. doi:10.1093/treephys/28.5.815. PMID:18316313.
- Mote, P.W., and Salathé, E.P. 2010. Future climate in the Pacific Northwest. *Clim. Change*, **102**(1–2): 29–50. doi:10.1007/s10584-010-9848-z.
- Mullineaux, D.R. 1986. Summary of pre-1980 tephra-fall deposits erupted from Mount St. Helens, Washington State, USA. *Bull. Volcanol.* **48**(1): 17–26. doi:10.1007/BF01073510.
- Pérez, F.L. 2009. The role of tephra covers on soil moisture conservation at Haleakala's crater (Maui, Hawai'i). *Catena*, **76**(3): 191–205. doi:10.1016/j.catena.2008.11.007.
- Peterson, D.W., and Peterson, D.L. 2001. Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology*, **82**(12): 3330–3345. doi:10.1890/0012-9658(2001)082[3330:MHGRTC]2.0.CO;2.
- Rho, H., Yu, D.J., Kim, S.J., and Lee, H.J. 2012. Limitation factors for photosynthesis in 'Bluecrop' highbush blueberry (*Vaccinium corymbosum*) leaves in response to moderate water stress. *J. Plant Biol.* **55**(6): 450–457. doi:10.1007/s12374-012-0261-1.
- Sade, N., Gebremedhin, A., and Moshelion, M. 2012. Risk-taking plants: anisohydric behavior as a stress-resistance trait. *Plant Signaling Behav.* **7**(7): 767–770. doi:10.4161/psb.20505.
- Schneider, C.A., Rasband, W.S., and Eliceiri, K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods*, **9**(7): 671–675. doi:10.1038/nmeth.2089.
- Scholander, P.F., Bradstreet, E.D., Hemmingsen, E.A., and Hammel, H.T. 1965. Sap pressure in vascular plants: negative hydrostatic pressure can be measured in plants. *Science*, **148**(3668): 339–346. doi:10.1126/science.148.3668.339. PMID:17832103.
- Seidling, W., Ziche, D., and Beck, W. 2012. Climate responses and interrelations of stem increment and crown transparency in Norway spruce, Scots pine, and common beech. *For. Ecol. Manage.* **284**: 196–204. doi:10.1016/j.foreco.2012.07.015.
- Siminovitich, D., and Cloutier, Y. 1983. Drought and freezing tolerance and adaptation in plants: some evidence of near equivalences. *Cryobiology*, **20**(4): 487–503. doi:10.1016/0011-2240(83)90037-8. PMID:6617235.
- Sproles, E.A., Roth, T.R., and Nolin, A.W. 2017. Future snow? A spatial-probabilistic assessment of the extraordinarily low snowpacks of 2014 and 2015 in the Oregon Cascades. *Cryosphere*, **11**: 331–341. doi:10.5194/tc-11-331-2017.
- Tappeiner, J.C., II, and Alaback, P.B. 1989. Early establishment and vegetative growth of understory species in the western hemlock–Sitka spruce forests of southeast Alaska. *Can. J. Bot.* **67**(2): 318–326. doi:10.1139/b89-046.
- Tejedor, M., Jiménez, C.C., and Díaz, F. 2002. Soil moisture regime changes in tephra-mulched soils. *Soil Sci. Soc. Am. J.* **66**(1): 202–206. doi:10.2136/sssaj2002.2020.
- Trujillo, E., Molotch, N.P., Goulden, M.L., Kelly, A.E., and Bales, R.C. 2012.

- Elevation-dependent influence of snow accumulation on forest greening. *Nat. Geosci.* **5**(10): 705–709. doi:[10.1038/ngeo1571](https://doi.org/10.1038/ngeo1571).
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., and Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. *Science*, **323**(5913): 521–524. doi:[10.1126/science.1165000](https://doi.org/10.1126/science.1165000). PMID: [19164752](https://pubmed.ncbi.nlm.nih.gov/19164752/).
- Vertessy, R.A., Benyon, R.G., O'Sullivan, S.K., and Gribben, P.R. 1995. Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiol.* **15**(9): 559–567. doi:[10.1093/treephys/15.9.559](https://doi.org/10.1093/treephys/15.9.559). PMID:[14965913](https://pubmed.ncbi.nlm.nih.gov/14965913/).
- Yi, K., Dragoni, D., Phillips, R.P., Roman, D.T., and Novick, K.A. 2017. Dynamics of stem water uptake among isohydric and anisohydric species experiencing a severe drought. *Tree Physiol.* **37**(10): 1379–1392. doi:[10.1093/treephys/tpw126](https://doi.org/10.1093/treephys/tpw126). PMID:[28062727](https://pubmed.ncbi.nlm.nih.gov/28062727/).
- Zobel, D.B. 1974. Local variation in intergrading *Abies grandis* – *A. concolor* populations in the central Oregon Cascades. II. Stomatal reaction to moisture stress. *Bot. Gaz.* **135**(3): 200–210. doi:[10.1086/336753](https://doi.org/10.1086/336753).
- Zobel, D.B., and Antos, J.A. 1991a. 1980 tephra from Mount St. Helens: spatial and temporal variation beneath forest canopies. *Biol. Fertil. Soils*, **12**(1): 60–66. doi:[10.1007/BF00369389](https://doi.org/10.1007/BF00369389).
- Zobel, D.B., and Antos, J.A. 1991b. Growth and development of natural seedlings of *Abies* and *Tsuga* in old-growth forest. *J. Ecol.* **79**(4): 985–998. doi:[10.2307/2261093](https://doi.org/10.2307/2261093).
- Zobel, D.B., and Antos, J.A. 1997. A decade of recovery of understory vegetation buried by volcanic tephra from Mount St. Helens. *Ecol. Monogr.* **67**(3): 317–344. doi:[10.1890/0012-9615\(1997\)067\[0317:ADOROU\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0317:ADOROU]2.0.CO;2).
- Zobel, D.B., and Antos, J.A. 2017. Community reorganization in forest understories buried by volcanic tephra. *Ecosphere*, **8**(12): e02045. doi:[10.1002/ecs2.2045](https://doi.org/10.1002/ecs2.2045).
- Zobel, D.B., and Antos, J.A. 2018. Forest understory buried by volcanic tephra: inertia, resilience, and the pattern of community re-development. *In Ecological responses at Mount St. Helens: revisited 35 years after the 1980 eruption. Edited by C.M. Crisafulli and V.H. Dale. Springer, New York. pp. 113–125. doi:10.1007/978-1-4939-7451-1_6.*