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Hydrometeorology organizes intra-annual patterns of tree growth across time, space and species in a montane watershed

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Summary

- Tree radial growth is often systematically limited by water availability, as is evident in tree ring records. However, the physiological nature of observed tree growth limitation is often uncertain outside of the laboratory.
- To further explore the physiology of water limitation, we observed intra-annual growth rates of four conifer species using point dendrometers and microcores, and coupled these data to observations of water potential, soil moisture, and vapor pressure deficit over 2 yr in the Northern Rocky Mountains, USA.
- The onset of growth limitation in four species was well explained by a critical balance between soil moisture supply and atmospheric demand representing relatively mesic conditions, despite the timing of this threshold response varying by up to 2 months across topographic and elevation gradients, growing locations, and study years.
- Our findings suggest that critical water deficits impeding tissue growth occurred at relatively high water potential values, often occurring when hydrometeorological conditions were relatively wet during the growing season (e.g. in early spring in some cases). This suggests that species-specific differences in water use strategies may not necessarily affect tree growth, and that tissue growth may be more directly linked to environmental moisture conditions than might otherwise be expected.

Key words: growth, hydraulic limitation, moisture supply and demand, soil moisture, soil–plant–atmosphere continuum, tree, vapor pressure deficit, water potential.

Introduction

That climate and tree growth are often tightly linked is a well-established and important principle shaping current, paleo, and future perspectives of both forest productivity (via modeling) and climate (via tree ring-based paleo-climate reconstructions). In arid and semi-arid regions world-wide, strong correlations between tree ring width and regional moisture conditions over annual to multi-decadal time periods highlight the role of water as a primary control on tree growth (Cook *et al.*, 2007, 2010; Stahle *et al.*, 2016). Water and plant growth are inextricably linked through transpiration and photosynthesis, with terrestrial productivity often being highly controlled by water availability (Rosenzweig, 1968; Biederman *et al.*, 2016). Trees act as conduits for moisture transport from Earth's surface to the atmosphere, with plants as a whole accounting for up to 64% of global evapotranspiration (Good *et al.*, 2015).

The general effects of climate on tree growth have been understood for centuries; however, the physiological mechanisms controlling radial growth are well hidden, occurring *beneath* the very tissues (phloem) that transport carbohydrates for growth. The tree rings that record this climate–growth relationship form via the process of xylogenesis. This includes cell division, cell expansion, and deposition of cell wall material (Lambers *et al.*, 2008).

While cell division does not lead to an appreciable size increase (Green, 1976), cell expansion may account for at least 80% of the size increase ultimately manifested as ring width. Deposition of cell wall material probably accounts for the majority of biomass added, but accounts for little size increase (Cuny *et al.*, 2015). While views on the role of cell division in growth continue to evolve (Beemster *et al.*, 2003), here we focus only on the size increase associated with cambial cell expansion (hereafter simply 'growth') while acknowledging that both cell division and expansion ultimately facilitate growth (Zahner, 1968).

Water limitation can influence radial growth via negative tensions generated in the xylem. General theory holds that newly divided cambial cells expand at a rate proportional to the difference between turgor pressure (Ψ_p ; MPa) and the minimum turgor required for cell wall extension (Ψ_y ; MPa) (Lockhart, 1965), although the process of expansion is further moderated by other factors including cell wall flexibility (Pritchard, 1994), biochemical signaling (Davies & Zhang, 1991), solute production (Michelela & Boyer, 1982), and the supply of water to developing tissues (Boyer *et al.*, 1985). During transpiration, water is moved upward from the soil and from within-tree storage reservoirs to the atmosphere, with the continuum maintained via capillary forces and cohesion between water molecules as water in the xylem replaces water lost from leaves (Dixon & Joly, 1894;

Pickard, 1981; Steppe *et al.*, 2006). This process is counterbalanced by gravity and by resistances within the xylem itself, generating negative hydrostatic pressure (tension) in the xylem stream, termed xylem water potential (Ψ_x). Under conditions of low water availability, the supply of water is probably the most important factor for cell expansion because of its direct role in maintaining $\Psi_p > Y$ in cells that are simultaneously expanding as a result of cell wall loosening. This hypothesis is supported by laboratory observations of immediate cessation of cell expansion in response to decreased Ψ_x even when Ψ_p of expanding cells is fully maintained (Boyer *et al.*, 1985; Nonami & Boyer, 1989, 1990).

In nature, Ψ_x is almost constantly changing as a consequence of variations in transpiration (Kaufmann, 1976) and can routinely reach highly negative pressures inducing stomatal regulation of Ψ_x to prevent cavitation (Sperry *et al.*, 1996; Sparks & Black, 1999). Both theory (Boyer & Silk, 2004) and modeling effort (Steppe *et al.*, 2006) suggest a tight linkage between Ψ_x and cambial cell expansion and hence growth. Mechanistically, Ψ_x should influence growth via the inhibition of cambial cell expansion by negative pressures present in adjacent xylem tissues (low Ψ_x), and evidence suggests that levels of Ψ_x that inhibit cell expansion are substantially less negative than those typically associated with the onset of stomatal regulation (Körner, 2015). This suggests that, at least in the early stages of drought, trees may consistently prioritize carbon uptake over growth by leaving stomata open at the expense of growth (which is inhibited by falling Ψ_x), thus leading to a decoupling of the two processes (Muller *et al.*, 2011).

In this study, we explore how low soil moisture supply and/or high atmospheric demand limits growth rates in four conifer species across a watershed. Furthermore, we explore if the growth response of trees to moisture supply and demand may be predictable and consistent across a range of species and hydrometeorological conditions. We report the findings of a field-based study with the aim of addressing the following objectives: to quantify the relationship between radial growth, soil moisture supply and atmospheric moisture demand; to compare our findings to existing evidence for how water potential (Ψ) controls radial growth; to determine the consistency of these relationships across environmental gradients and among different tree species.

Materials and Methods

Study design and sampling

This study was conducted over the 2014 and 2015 growing seasons at the Lubrecht Experimental Forest in western Montana, USA, in a mixed coniferous forest of the Northern Rockies. Four sites were selected within smaller subcatchments of the North Fork Elk Creek watershed to capture hydrometeorological variation from high (c. 1750 m above sea level (asl)) to low (c. 1400 m asl) elevations as well as across north-, south- and west-facing aspects. Soil types within the study area range from gravely loamy sands to gravely sandy loams, although soils are heterogeneous even within sites as a result of the complexity of the mountainous

terrain and the variability of soil depths (NRCS, 2017). One site was omitted from the analysis because of severe canopy defoliation by western spruce budworm (*Choristoneura occidentalis*) during both study years. Within each site, we sampled trees representing differing topographic positions; we selected four trees from convergent, hollow locations and four trees from more divergent slope locations (Table 1), with tree selection dictated by the proximity to a central data-logger. Tree species sampled included Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco), ponderosa pine (*Pinus ponderosa* P. & C. Lawson), western larch (*Larix occidentalis* Nutt.), and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm). We measured stem radii using two point dendrometers installed at breast height on each of 24 trees for a total of 48 sensors in the study (see Wang & Sammis, 2008 for dendrometer design and calibration details). Stem radius readings were logged using CR1000 data-loggers (Campbell Scientific Inc., Logan, UT, USA). Central to each topographic grouping of trees, we recorded air temperature and relative humidity with a VP3 temperature and humidity sensor, and soil volumetric water content (VWC_{soil}) at 50 cm depth using 5TE sensors and EM50 data-loggers (Decagon Devices Inc., Pullman, WA, USA).

All trees were sampled for cellular analysis of growth to compare against automated measurements of stem radius from dendrometers. During 2015, a total of 216 microcores were collected at biweekly intervals from near the dendrometer on each tree. Microcores were then fixed, embedded in paraffin, and sectioned to a thickness of 8 μ m for microscopic analysis of developing cells (Rossi *et al.*, 2006a).

Table 1 Site location, species, topographic position and diameter at breast height (DBH) of trees in the study

Site	Species	Topographic position	DBH (cm)
Driest	Douglas-fir	Hollow	26.2
	Douglas-fir	Hollow	38.2
	Douglas-fir	Slope	31.0
	Douglas-fir	Slope	35.8
	Ponderosa pine	Hollow	43.0
	Ponderosa pine	Hollow	56.3
	Ponderosa pine	Slope	24.4
	Ponderosa pine	Slope	42.1
Intermediate	Douglas-fir	Hollow	50.4
	Douglas-fir	Hollow	56.0
	Douglas-fir	Slope	32.0
	Douglas-fir	Slope	36.8
	Western larch	Hollow	27.6
	Western larch	Hollow	38.1
	Western larch	Slope	29.0
	Western larch	Slope	56.9
Wettest	Douglas-fir	Hollow	52.5
	Douglas-fir	Hollow	64.6
	Douglas-fir	Slope	22.2
	Douglas-fir	Slope	24.5
	Engelmann spruce	Hollow	56.5
	Engelmann spruce	Hollow	67.2
	Engelmann spruce	Slope	22.1
	Engelmann spruce	Slope	78.1

In all species except western larch, we measured predawn and midday stem water potential, Ψ_{pre} and Ψ_{mid} (MPa), respectively, three times in 2014 (June, July and August). For each tree, the tip of a sunlit branch was cut with a pole pruner and inserted into a pressure chamber (Model 600; PMS Instrument Co., Albany, OR, USA; Scholander *et al.*, 1965). Because we did not measure water potentials in western larch, this species was excluded from all analyses incorporating water potential measurements.

Estimation of growth

All analyses were constrained to the ‘growing season’, defined as a period of 140 d beginning on 4 May 2014 and 15 April 2015. For each year, this time interval visually captured the period of cambial cell expansion in all trees evident from the dendrometer records and supported by observations of xylogenesis using microcores.

We estimated seasonal growth curves from dendrometers in individual trees from all-time daily radius maxima. Growth estimates made at daily maxima generally provide an accurate estimate of growth provided that no underlying water deficit in the tree simultaneously limits stem radius. Of concern was the effect that cumulative tree water deficits could have on the estimation of seasonal growth over time. To address this, we compared growth curves estimated from dendrometers to observations of xylogenesis made using microcores. Because we were only able to collect microcores for half of the 2014 season, this analysis was restricted to the 2015 growing season.

We found stem radii measured from thin sections of microcores (μm) to correlate with radii measured with dendrometers (μm) ($r=0.89$ and a slope of 1.27 with dendrometers consistently overestimating stem radial increments). This is consistent with the fact that the dendrometers measure newly formed xylem and phloem cells while we quantified only new xylem cells using microcores. We assessed whether cumulative water deficits affected the relationship between dendrometers and microcores over time by comparing the fits of linear and quadratic models relating the two measurements. We reasoned that a linear relationship between dendrometers and microcores reflected a consistent relationship between the measurements, while a curved relationship, caused by cumulative water deficit in the stem over time, reflected a divergence between the two measurements. In all cases, we found a consistent linear relationship over the growing season. An exception to this was the observation that, at the very start of the growing season, some radii increased a small amount before xylogenesis was observed in microcores.

Quantification of moisture supply and demand

Using the half-hourly measurements of air temperature and relative humidity, we quantified the evaporative demand of the atmosphere as vapor pressure deficit (VPD; kPa):

$$\text{VPD} = e_{(T)} - e_{(T)} \times \text{RH}/100 \quad \text{Eqn 1}$$

($e_{(T)}$, the saturation vapor pressure at air temperature T (K); RH (%), relative humidity.) Following (Tetens, 1930) $e_{(T)}$ was calculated as

$$e_{(T)} = 0.6108 \times \exp[17.27 T / (T + 237.3)] \quad \text{Eqn 2}$$

We estimated moisture supply as the volumetric water content of soil (VWC_{soil}) at a depth of 50 cm.

In addition to stomatal regulation, Ψ is strongly controlled by the moisture gradient resulting from the difference between soil moisture supply and atmospheric demand (VPD) (Dixon & Joly, 1894; Scholander *et al.*, 1965). Here we utilize a simple proxy for the combined influence of soil moisture supply and atmospheric demand on the soil–atmosphere system termed the hydrometeorologic dryness index (HDI; $\text{kPa m}^{-3} \text{H}_2\text{O m}^3 \text{soil}$) and defined as:

$$\text{HDI} = \text{VPD} / \text{VWC}_{\text{soil}} \quad \text{Eqn 3}$$

Here, VPD captures the atmospheric demand for moisture by quantifying the absolute water concentration difference between the leaf and the atmosphere, with the tree’s ability to maintain turgor depending on its moisture supply (soil water). Thus, HDI modifies the demand term (VPD) by dividing it by a measure of soil moisture (VWC_{soil}) to reflect the increasing difficulty for the tree to maintain turgor with decreasing soil moisture.

Previous authors have applied an Ohm’s law approach to link hydrometeorology to plant water relations (e.g. Steppe *et al.*, 2006). In this context, surface to atmosphere flow of water is proportional to a water potential difference between soil and atmosphere divided by the total resistance to flow along the soil–plant–atmosphere continuum. However, data needed to quantify flow, the surface–atmosphere water potential difference, and other resistances present in the flow path are not trivial to collect, especially in a field study. While HDI does not replace a mechanistic model such as an Ohm’s law analogy for quantifying components of the complex soil–plant–atmosphere system, its component data are relatively easy to collect and serve as a simple proxy for water flow through the soil–plant–atmosphere continuum. As conditions dry, an increasing atmospheric moisture demand is met by a decreasing soil moisture supply, which leads to an exponential increase in HDI and drives Ψ to be more negative in trees. It is important to consider that, because soil moisture supply is partly a function of soil water retention characteristics in addition to moisture content, observed relationships between Ψ and HDI may be soil-specific. In addition, stomata also act to regulate Ψ and increasingly limit the influence of HDI on Ψ as conditions dry. Because stomatal responses vary by species, we assessed species-specific relationships between Ψ and HDI.

To provide a general visualization of the topographic and spatial variability of HDI, we related observed soil moisture to the topographic wetness index (TWI) (Beven & Kirkby, 1979), elevation (m), and summer solstice solar insolation

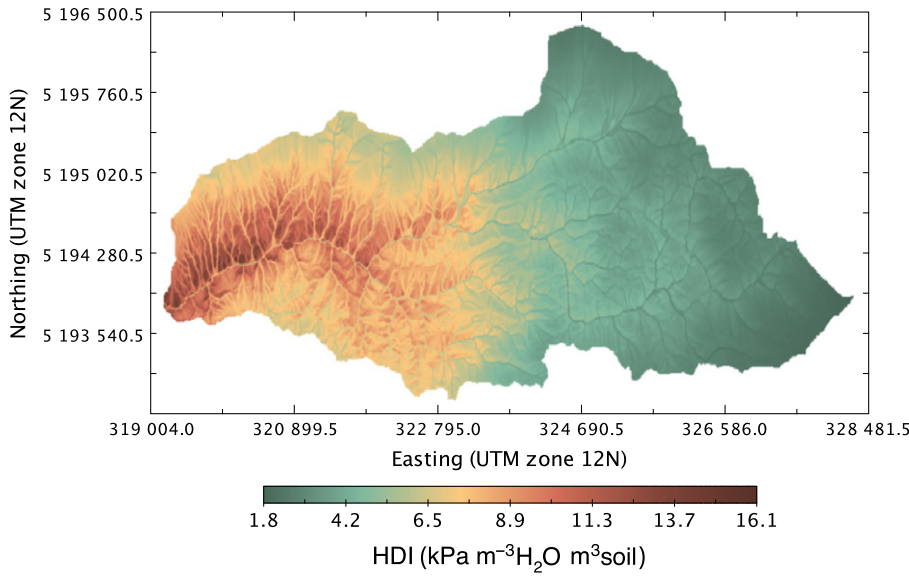


Fig. 1 The spatial distribution of the average growing season hydrometeorologic dryness index (HDI) for 2014 and 2015 modeled by multiple linear regression from point observations of soil moisture and vapor pressure deficit in relation to radiation, elevation, and the topographic wetness index (TWI) within the North Fork Elk Creek watershed.

(W m^{-2}) (Bird & Hulstrom, 1981; Corripio, 2014) and related VPD to elevation at each of eight micro-meteorological stations in the watershed by multiple/linear regression. We then calculated HDI for each grid cell in the watershed using a 10-m digital elevation model (Fig. 1). Over both growing seasons, modeled VPD, VWC_{soil} , and HDI described an average of 91.0%, 20.0% and 73.3%, respectively, of the spatial variation in observed values of VPD, VWC_{soil} and HDI on a daily basis. While the spatial variability in VPD was well explained by elevation alone, the variability in soil moisture present across the complex topography of the study area was more difficult to model.

We categorically defined the three different study sites within the watershed as ‘dry’, ‘intermediate’ and ‘wet’ based on the observed seasonal average value of HDI at each site (Fig. 2). The driest site was lowest in elevation and faced predominantly south, while the intermediate site was slightly higher in elevation and faced predominantly northwest, and the wettest site was highest in elevation and faced predominantly southwest.

Extraction of low-frequency signals from time series data

Both stem radius and HDI time series were extremely noisy over daily intervals as both reflect diurnal swings in microclimatic conditions and weather. While it is unclear at exactly what frequency the mechanics of growth respond to hydrometeorology, our aim was to generally quantify this response over the course of the growing season. To extract the low-frequency features of each time series, we applied a low-pass filter to both HDI and stem radius using a cubic smoothing spline implemented in R (R Core Team, 2013) using package `DPLR` (Cook & Kariukstis, 1990; Bunn, 2008).

We filtered stem radius time series with the most flexible spline possible that resulted in a single inflection point in the annual growth curve of each tree. The form of each resulting time series generally approximated the Gompertz function commonly used

to fit annual tree growth curves (Zeide, 1993; Rossi *et al.*, 2006b). This process facilitated the calculation of growth rate (stem radius increment (SRI); $\mu\text{m d}^{-1}$) curves with a single local maximum over the growing season (Fig. 3). The minimum period necessary to produce a filtered growth curve with a single inflection point ranged from 27 to 119 d over all trees and both study years.

In choosing a low-pass filter to smooth the HDI time series, we sought to match the frequency used to filter stem radius time series. To minimize subjectivity in the process of filtering HDI, we generated 100 different filtered HDI time series with spline periods ranging from 5 to 105 d. This centered the range of periods on the mean period used to filter all radii, which was 55 d, and which we used for further analyses. We then quantified the amount of uncertainty associated with the estimation of HDI resulting from the smoothing process alone (horizontal error bars in Fig. 4d).

Calculation of growth rates (SRI), maximum growth (SRI_{max}), and HDI_{crit}

We quantified growth as the observed SRI from filtered stem radius time series where growth is greater than zero only when the maximum stem radius achieved in a given day is greater than the all-time previous maximum (Zweifel *et al.*, 2016). In order to estimate daily SRI from growing season stem radius curves, we calculated the discrete derivative of filtered stem radius time series as:

$$\text{SRI} = \text{radius}^t - \text{radius}^{t-1} \quad \text{Eqn 4}$$

(SRI, the change in radius from time $t-1$ to time t in units of $\mu\text{m d}^{-1}$ (Fig. 3a).) Because we filtered each stem radius time series to contain only one inflection point, its derivative contained only one local maximum (Fig. 3b). We interpreted this

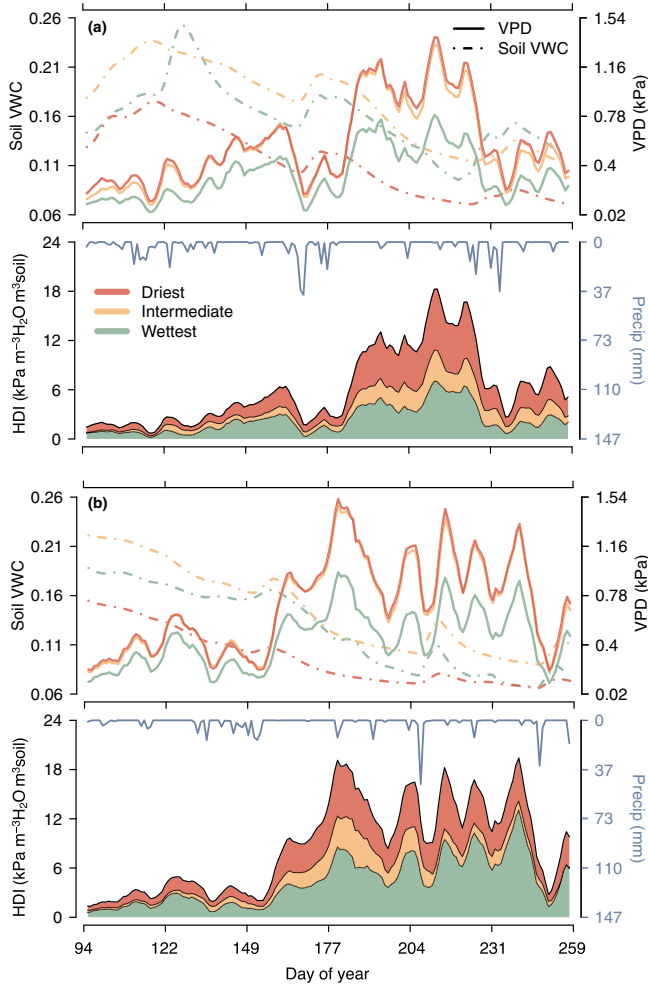


Fig. 2 Time series of soil water content (VWC), atmospheric vapor pressure deficit (VPD) and average daily hydrometeorologic dryness index (HDI) at each of the three study sites (driest, intermediate, and wettest) during the (a) 2014 and (b) 2015 growing seasons. Rainfall averaged across all sites is also shown on the reversed right axis. For clarity, all data except rainfall are shown as 5-d moving averages.

maximum value of SRI as the maximum daily growth rate (SRI_{max}) observed during the growing season with all values of SRI following this maximum representing the ‘growth limitation’ phase of the SRI time series.

In order to estimate the hydrometeorological conditions under which the rate of radial growth decreased, we estimated the corresponding HDI value (HDI_{crit}) associated with SRI_{max} by averaging the values of HDI experienced by all trees on the day each tree reached SRI_{max} (Fig. 3). We found that, across the landscape and among the four different species, the average HDI_{crit} was $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil} \pm \text{SE of } 0.22$. We further evaluated the timing of SRI_{max} (τSRI_{max} ; day of year) and HDI_{crit} (τHDI_{crit} ; day of year) as follows: we defined the day on which each tree reached its maximum growth rate during the season (τSRI_{max}) as the day on which that tree expressed SRI_{max} and we defined τHDI_{crit} as the day on which daily average HDI first exceeded a value of $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil}$ (Fig. 3).

Analyses of the τSRI_{max} vs τHDI_{crit} relationship

Exploratory analyses revealed a close relationship in time between τSRI_{max} and τHDI_{crit} . We tested the strength of this relationship and its dependence on factors such as average site moisture conditions, topography, study year, and species using a linear model. Within this framework, we expected a close relationship between τSRI_{max} and τHDI_{crit} to be characterized by a slope coefficient (β_1) close to 1 and a high r^2 . We compared a suite of additive and nonadditive models based on the general nonadditive form of $\mu\{\tau SRI_{max}|\tau HDI_{crit}\} = \beta_0 + \beta_1 \times \tau HDI_{crit} + \beta_2 \times \text{FACTOR} + \beta_3 \times \tau HDI_{crit} \times \text{FACTOR} + e$, where the mean of τSRI_{max} given τHDI_{crit} is explained by the linear combination of τHDI_{crit} , factor, and the interaction of the two. We assessed support for separate estimations of β_1 for different levels of site, topography, study year, and species by comparing additive and nonadditive models for each factor using F -tests, and report the variance in τSRI_{max} explained by τHDI_{crit} as the squared correlation between τSRI_{max} and τHDI_{crit} within individual factor levels as well as the variance explained across all factors.

Assessing the effect of growing season HDI on average daily growth rates

We explored the cumulative effect of growing season moisture stress on growth by examining the relationship between the proportion of time during the growing season that average daily HDI remained above HDI_{crit} (αHDI_{crit}) and average seasonal SRI. Comparing absolute growth in trees is difficult because of the number of confounding factors that also influence individual tree radial growth (e.g. ontogeny, genetics, competition, and leaf area). To compensate for this, we averaged growth rates of trees in each topographic position within each site to amplify site-specific growth signals responding to a common condition of HDI. We also determined the effect of tree size (diameter at breast height (DBH)) on the relationship by comparing nonlinear models with and without DBH using a likelihood ratio test (Huet *et al.*, 2006). Finding little evidence for an effect of DBH on radial growth among trees studied ($P = 0.19$; $\lambda = 1.71$; $df = 1$), we regressed these mean growth rates on αHDI_{crit} by nonlinear least-squares regression (NLSR) using the ‘NLSLM’ function in the R package ‘MINPACK’ (Elzhov *et al.*, 2016) and verified the goodness of fit by leave-one-out cross-validation. We could not assess how the growing conditions of the previous year may have influenced current year growth given the duration of our study (e.g. Zielis *et al.*, 2014). However, the modeled relationship between αHDI_{crit} and growth is a good fit for both years despite a considerable increase in αHDI_{crit} in 2015. Nonetheless, some errors caused by annual carry-over effects on growth may be present in the analysis.

Converting Ψ_{pre} and Ψ_{mid} to Ψ

While we were unable to directly measure Ψ_x , we were able to make branch-level measurements of predawn (Ψ_{pre}) and midday (Ψ_{mid}) water potential. We sampled twigs for Ψ_{pre} and Ψ_{mid} from

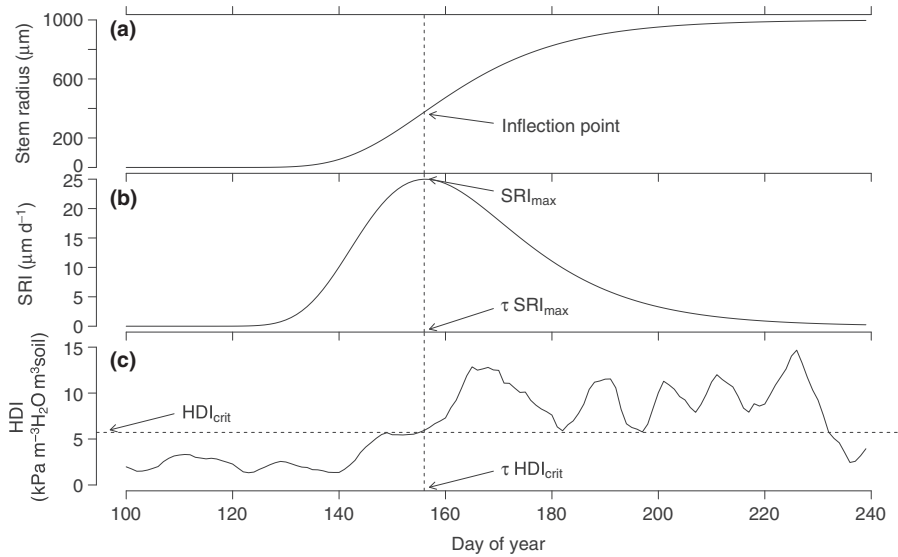


Fig. 3 Conceptual diagram showing the relationship between (a) a smoothed annual growth curve, (b) its derivative (stem radius increment (SRI)), and (c) the hydrometeorologic dryness index (HDI). SRI_{max}, maximum rate of SRI; τSRI_{max}, day of year when SRI_{max} is reached; τHDI_{crit}, day of year when the critical value of HDI (HDI_{crit}) associated with SRI_{max} is reached.

c. 5.5 m above the dendrometers in order to estimate a proxy for water potential at the dendrometer (hereafter simply Ψ). One can account for the effect of gravity on Ψ as a decrease of 0.01 MPa in Ψ for each 1-m increase in stem height (Scholander *et al.*, 1965). However, additional resistances resulting from the flow of water through xylem can generate larger vertical gradients in Ψ . From a survey of the literature (Hellkvist *et al.*, 1974; Hinckley *et al.*, 1978; Bauerle *et al.*, 1999; Woodruff *et al.*, 2004), we found considerable variation in Ψ gradients and, in some cases, the variation within a single species exceeded the variation observed among different species. Given this variation, we estimated a mean gradient for converting Ψ_{mid} to Ψ from all available literature estimates (17 in all), multiplied this gradient by 5.5 m, and added this to the observed value of Ψ_{mid} . This mean gradient estimate was equal to $0.0634 \pm 0.0143 \text{ MPa m}^{-1}$. The mean value for gradients of Ψ_{pre} from the literature was $0.0046 \text{ MPa m}^{-1}$ lower than that of Ψ_{mid} , and thus we used a value of 0.0588 for the gradient of Ψ_{pre} (Bauerle *et al.*, 1999; Woodruff *et al.*, 2004). While these studies suggest that vertical gradients in water potential larger than those expected from gravity alone can exist in trees even during the pre-dawn, theory predicts that only the gravitational effect on Ψ should persist when flow in the tree ceases. As we did not quantify flow in the study trees, some error may exist in our estimate of Ψ at times.

Modeling Ψ from HDI and estimating Ψ_{crit} at $\text{HDI} = \text{HDI}_{\text{crit}}$

In order to explore the mechanistic link between observed growth limitation and hydrometeorology, we estimated seasonal time series of average daily Ψ based on concurrent measurements of HDI. We modeled Ψ from observed HDI by fitting a negative exponential function, by NLSR as described for the modeling of average daily SRI from $\alpha \text{HDI}_{\text{crit}}$. The function form reflected the expected shape of the relationship based on theory (increasing slope of Ψ -HDI with increasing HDI as a result of increasing stomatal regulation of Ψ). We assessed the goodness of fit for

species-specific models via a leave-one-out cross-validation procedure. We assessed the importance of species differences in the fit of the relationship by comparing the summed log likelihoods from models fit to data subset by species to the full model including data from all species using a likelihood ratio test (Huet *et al.*, 2006).

To estimate Ψ_{crit} , we evaluated the function for each species at a value of $\text{HDI} = \text{HDI}_{\text{crit}}$ and generated 95% confidence intervals for the estimates by Monte Carlo simulations using the PREDICTNLS function from the R package 'PROPAGATE' (Spiess, 2014).

Results

Spatiotemporal variability in HDI and its constituent variables

Topographic features and seasonal changes in weather generated considerable variation in the magnitude of HDI within the watershed. Point measurements of HDI ranged from 0 to c. 100 during the study, with HDI equal to 0 when RH equaled 100%. Spatial variation in average growing season HDI modeled from point observations over both study years is shown for the North Fork Elk Creek watershed in Fig. 1. HDI tended to be higher at lower elevations, on more southerly aspects, and in more divergent topographic positions. HDI was also much higher during the day than at night. The magnitude and temporal distribution of HDI were similar in the two study years but the onset of summer-like conditions was delayed by c. 20 d in 2014 relative to 2015 (Fig. 2).

Because HDI is the quotient of two variables, VPD and soil moisture, it is difficult to assess the ecologically meaningful contribution of each variable independently over the course of a growing season, especially as VPD and soil moisture sometimes drive variability in HDI independently, and at other times (more often) in concert. However, in a post hoc analysis, we held either

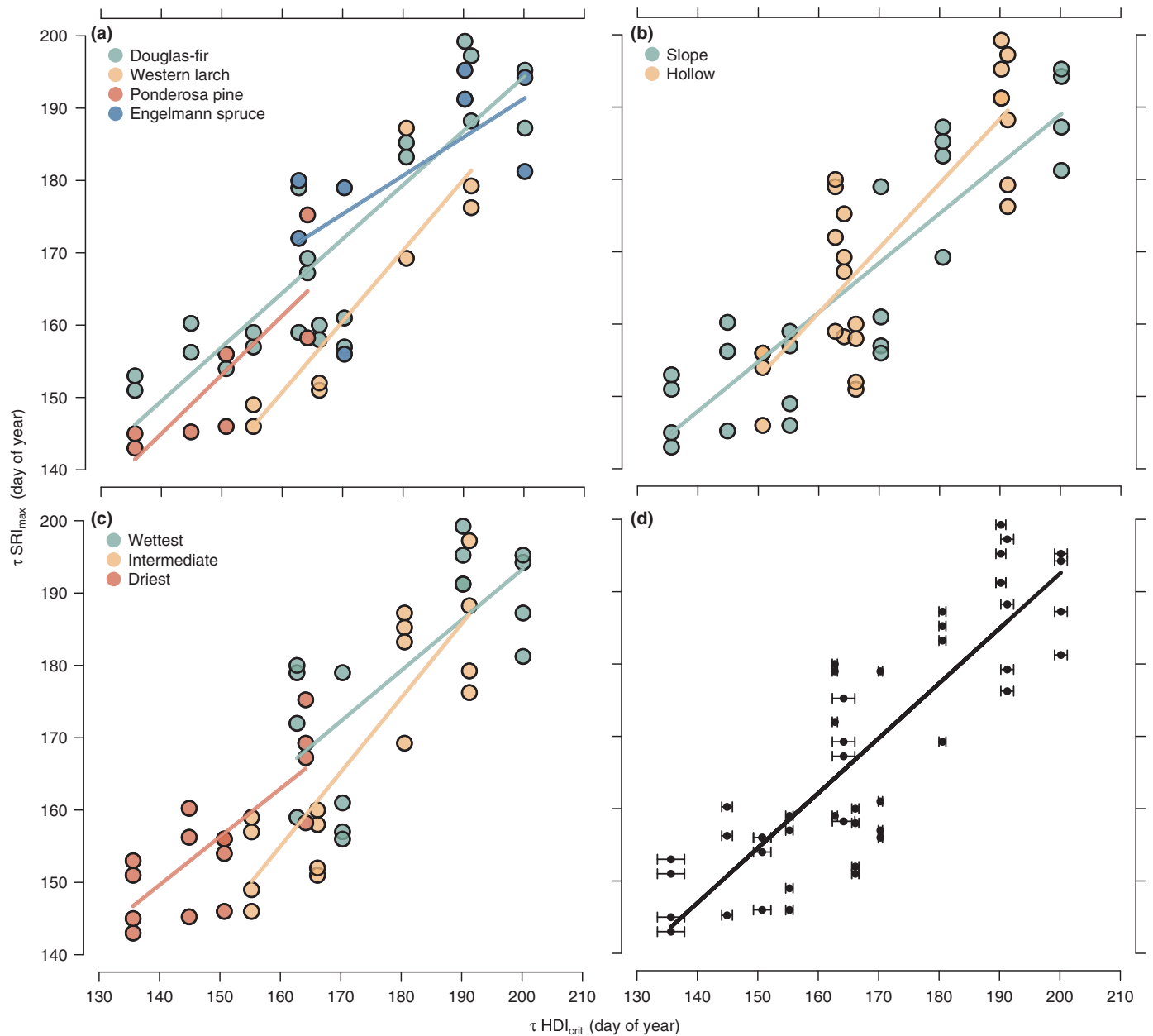


Fig. 4 The day of the year on which average daily hydrometeorologic dryness index (HDI) first exceeded $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil}$ ($\tau\text{HDI}_{\text{crit}}$) vs the day on which daily growth rates peaked ($\tau\text{SRI}_{\text{max}}$) for all study trees over both years. Color and regression lines depict groups of trees and the fitted line for each group based on (a) species, (b) topographic position and (c) site. Error bars show $\pm 2 \text{ SEM}$ for $\tau\text{HDI}_{\text{crit}}$ from the full suite of splines used to filter HDI (d). Species shown include Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco), ponderosa pine (*Pinus ponderosa* P. & C. Lawson), western larch (*Larix occidentalis* Nutt.), and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm).

VPD or soil moisture constant at its observed seasonal mean while assessing average HDI in the watershed at each point observation of the complementary variable. This allowed us to estimate how often VPD or soil moisture alone might drive HDI above HDI_{crit} . In so doing, we estimated that soil moisture levels alone would be enough to surpass the HDI_{crit} threshold 48% of the time vs only 32% of the time for VPD. This is somewhat counterintuitive, as short-term variation in HDI is almost entirely driven by VPD. However, high VPD levels are transient, giving way to high humidity and low temperatures most nights. Furthermore, because soil moisture changes much more slowly

than VPD, it serves to slowly modulate the effect of VPD on HDI over the course of the growing season, driving HDI exponentially higher in response to VPD as soil water evaporates (Fig. 5).

The response of growth to HDI, the timing of maximum growth, and the onset of growth limitation

Across a heterogeneous landscape with differing microtopography, daily growth rates of all four trees species increased sharply in response to increasing daily average HDI, but growth

slowed as HDI surpassed a daily average value of c . $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil}$. Growth then decreased as conditions dried, to a point where daily growth approached zero when average daily HDI exceeded $20 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil}$. The importance of 5.72 as an HDI threshold value for growth was evident when assessing the timing of peak growth in trees during the growing season. The statistics for the regression analyses of $\tau\text{SRI}_{\text{max}}$ on $\tau\text{HDI}_{\text{crit}}$ are shown in Table 2. Even though the day of year of maximum growth rates varied by up to 2 months in different locations over the two study years, $\tau\text{HDI}_{\text{crit}}$ alone described 73% of the variation in $\tau\text{SRI}_{\text{max}}$ (Fig. 4d). We estimated the slope of $\tau\text{SRI}_{\text{max}}/\tau\text{HDI}_{\text{crit}}$ (β_1) at 0.76 ± 0.069 including all trees. We found little evidence that β_1 varied across differences in species, average site moisture conditions, topographic positions, and study years (F -tests, $\alpha = 0.05$; Table 2) (Fig. 4a–c). In 2015, the mean $\pm$ SE of $\tau\text{HDI}_{\text{crit}}$ for all trees was 23.2 ± 4.4 d earlier than that of 2014 and, similarly, the mean of $\tau\text{SRI}_{\text{max}}$ for all trees was 22.2 ± 3.7 d earlier in 2015 than 2014.

When trees were aggregated by site and topographic position, their seasonally averaged mean daily growth rates exhibited a nonlinear relationship with the proportion of time that HDI exceeded HDI_{crit} ($\alpha\text{HDI}_{\text{crit}}$) (Fig. 6). This relationship was approximated by the function:

$$\text{SRI} = \text{SRI}_{\text{max}} - a \times e^{(k \times \alpha\text{HDI}_{\text{crit}})} \quad \text{Eqn 5}$$

(SRI_{max} , the estimated average maximum value of SRI for all sites; a , a constant; k , the rate constant for SRI_{max} .) We estimated a , k , and SRI_{max} to be 0.28 ± 0.36 , 4.48 ± 1.62 , and 18.69 ± 1.06 (mean $\pm$ SE), respectively. We estimated the cross-validation r^2 for the model to be 0.61 using a leave-one-out cross-validation approach. Fig. 6 shows that the relationship is not linear; growth rates are relatively unaffected until trees spend approximately half of their time above HDI_{crit} , after which growth rates decline exponentially with a decrease in the estimated time suitable for cell expansion.

The response of Ψ to HDI and species estimates of Ψ_{crit}

Water potential (Ψ) decreased with increasing HDI as approximated by a negative exponential function of the form:

$$\Psi = \Psi_{\text{max}} \times e^{(-k \times \text{HDI})} \quad \text{Eqn 6}$$

(Ψ_{max} , the estimated average maximum value of Ψ for a given species within the range of observed HDI; k , the rate constant for Ψ .) This general relationship between HDI and Ψ shows that, as moisture conditions become drier (from either drying soils or drying atmosphere), trees experience more negative water potentials and water stress. This tendency is inversely asymptotic at higher values of HDI, as is expected as a result of regulation of Ψ by stomata (Fig. 7). The response of Ψ to HDI varied slightly by species ($P = 0.002$ from a likelihood ratio test; $\lambda = 20.49$; $\text{df} = 6$). Cross-validation r^2 from a leave-one-out procedure for species-specific models for Douglas-fir, Englemann spruce, and ponderosa pine was 0.71, 0.39, and 0.71, respectively.

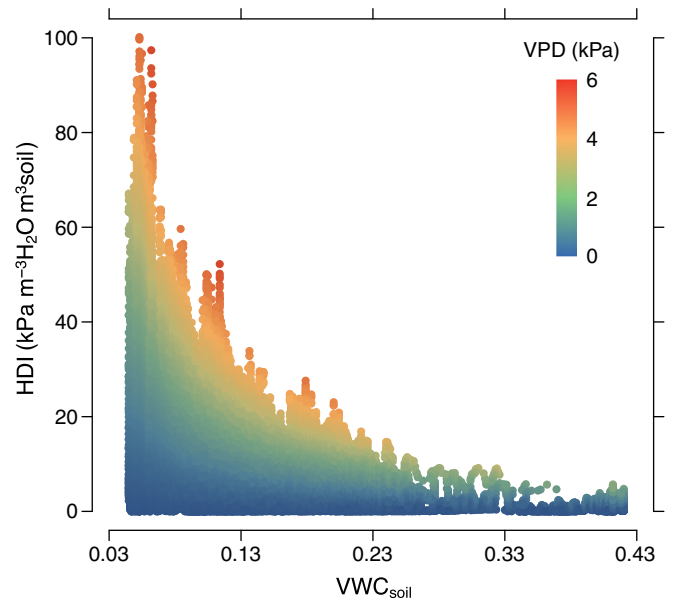


Fig. 5 The 2014 and 2015 growing season point observations of the hydrometeorologic dryness index (HDI) vs soil moisture (VWC_{soil}) color coded by vapor pressure deficit (VPD).

The shape of the relationship for each species determined its individual estimate of Ψ_{crit} by evaluation of Ψ at HDI_{crit} . We estimated Ψ_{crit} based on a common HDI_{crit} value across species because the mean estimate of HDI_{crit} was statistically equivalent for these different species ($\text{HDI}_{\text{crit}} = 5.76 \pm 0.21$ (mean $\pm$ SE); $F = 0.143$; $\text{df} = 2$ and 36; $P = 0.87$). This suggests that growth limitation in all tree species began in unison in response to hydrometeorological conditions despite species' physiological differences. Species-specific parameter estimates for the relationships as well as estimates for Ψ_{crit} are shown in Table 3. Douglas-fir exhibited the lowest water potentials across its range of HDI followed by ponderosa pine. Englemann spruce experienced a more limited range of HDI, which resulted in more uncertainty in the model fit for this species, yet Englemann spruce maintained the highest potentials of all species across this range (Fig. 7).

Discussion

In this study, we addressed hydrometeorological controls on *intra*-annual growth dynamics across a complex watershed and among different tree species with different physiological responses to water availability. We found that the onset of growth limitation in trees was tightly controlled by changes in hydrometeorology; specifically, we found that all four conifer species expressed limitation in growth when HDI exceeded $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil}$ (HDI_{crit}) (Fig. 4). At an HDI of $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil}$, atmospheric demand combined with soil moisture supply generated moderate hydraulic tension in transpiring trees, resulting in Ψ ranging from -0.71 to -0.91 MPa depending on species (Fig. 7). This relationship was established based on real-time measurements of HDI concurrent with Ψ , which varied across the season as a consequence of species-specific traits and topographic controls on

Table 2 Regression analysis and *F*-test statistics for the estimation of the timing of maximum growth ($\tau\text{SRI}_{\text{max}}$) vs the timing of the estimated growth threshold value of the hydrometeorologic dryness index ($\tau\text{HDI}_{\text{crit}}$)

Factor ¹	Level	Estimate ²	SE	df	Res. df	<i>F</i>	<i>t</i>	<i>P</i> > <i>F</i>	<i>P</i> > <i>t</i>	<i>r</i> ²
$\tau\text{HDI}_{\text{crit}}:\text{species}$				3	39	0.850		0.475		
	Engelmann spruce	0.531	0.192	39			2.770		0.009	0.43
	Ponderosa pine	0.814	0.281	39			2.900		0.006	0.69
	Douglas-fir	0.747	0.088	39			8.532		< 0.001	0.79
	Western larch	0.980	0.210	39			4.673		< 0.001	0.80
$\tau\text{HDI}_{\text{crit}}:\text{year}$				1	43	1.590		0.214		
	2014	0.707	0.099	43			7.173		< 0.001	0.74
	2015	0.482	0.149	43			3.232		0.002	0.29
$\tau\text{HDI}_{\text{crit}}:\text{position}$				1	43	2.054		0.159		
	Hollow	0.894	0.121	43			7.398		< 0.001	0.69
	Slope	0.683	0.084	43			8.155		< 0.001	0.79
$\tau\text{HDI}_{\text{crit}}:\text{site}$				2	41	1.510		0.233		
	Driest	0.666	0.207	41			3.220		0.003	0.61
	Intermediate	1.026	0.155	41			3.220		< 0.001	0.77
	Wettest	0.700	0.142	41			4.923		< 0.001	0.53
None ³	All levels	0.759	0.069	45			11.075		< 0.001	0.73

¹Interaction terms between $\tau\text{HDI}_{\text{crit}}$ and factors species, year, position and site, for which support was assessed via *F*-tests.

²Estimated slope of $\tau\text{SRI}_{\text{max}}$ vs $\tau\text{HDI}_{\text{crit}}$ (β_1) (d) for each factor level given the general nonadditive model of form $\mu\{\tau\text{SRI}_{\text{max}}|\tau\text{HDI}_{\text{crit}}\} = \beta_0 + \beta_1 \times \tau\text{HDI}_{\text{crit}} + \beta_2 \text{factor} + \beta_3 \times \tau\text{HDI}_{\text{crit}} \times \text{factor}$.

³Regression statistics for the reduced model $\mu\{\tau\text{SRI}_{\text{max}}|\tau\text{HDI}_{\text{crit}}\} = \beta_0 + \beta_1 \times \tau\text{HDI}_{\text{crit}}$.

hydrometeorology. These water potential values represent possible threshold values in which xylem expansion is inhibited, thereby resulting in decreased growth rates. The strong relationship between HDI and growth was consistent across species and at different landscape positions (Fig. 4), suggesting that HDI may be a useful variable for predicting the onset of forest growth limitation both in time and in space (Fig. 4).

The relationship between radial growth and HDI

We found a strong relationship between radial growth and HDI among all four tree species. Although the range of HDI was larger for species growing in drier landscape positions (e.g. Douglas-fir and ponderosa pine) compared with species growing in more mesic landscape positions (e.g. western larch and Engelmann spruce), different species converged on a similar value of HDI_{crit} . Such a finding is surprising, but not unprecedented. For example, in a northern boreal forest, trees from multiple genera were observed to synchronize the timing of maximum growth around the occurrence of the summer solstice when the photoperiod was longest (Rossi *et al.*, 2006b).

At the driest locations in the watershed, daily average HDI exceeded HDI_{crit} as early as mid-May and remained above HDI_{crit} for much of the growing season (Fig. 2). Radial growth peaked from mid-May to early June, which is consistent with other dendrometer-based reports of radial growth phenology in trees from similar elevations and latitudes (Zweifel *et al.*, 2006; Cuny *et al.*, 2015). The time that HDI exceeded HDI_{crit} ($\tau\text{HDI}_{\text{crit}}$) varied by up to 2 months across the landscape and the two study years. However, $\tau\text{HDI}_{\text{crit}}$ described 73% of the variation in the timing of peak growth ($\tau\text{SRI}_{\text{max}}$) (Fig. 4). In addition, the variables used to calculate HDI (temperature, humidity and volumetric soil moisture) are predictably influenced by local

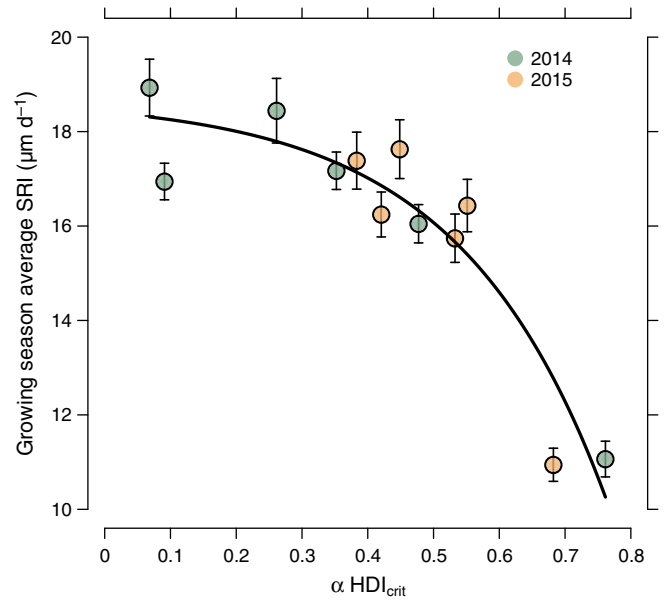


Fig. 6 The relationship between the proportion of days during the growing season in which average hydrometeorologic dryness index (HDI) was above its threshold value of $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil}$ ($\alpha\text{HDI}_{\text{crit}}$), and the mean daily growth rate (SRI) for each study plot over both years. Error bars depict $\pm 1 \text{ SEM}$.

topography (Beven & Kirkby, 1979; Bonan, 2002) (Fig. 1). This suggests that the topographic structure of the landscape may serve to organize patterns of tree growth across a particular region. As such, combinations of HDI and topographic information such as elevation and curvature may serve as generally applicable tools for understanding the spatial distributions of forest growth dynamics in water-limited systems, and where covariance between topography and other growth-limiting variables is understood.

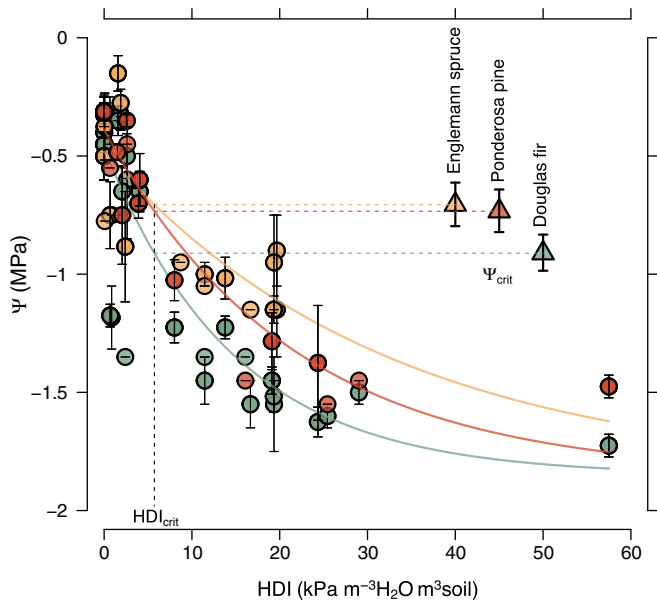


Fig. 7 The relationship between the hydrometeorologic dryness index (HDI) and xylem water potential (Ψ) estimated from repeated stem water potential measurements across time and a range of moisture conditions. Circles represent the mean of each species ($n = 4$ trees) per sampling from each sampling location with error bars showing ± 1 SEM. Triangles represent estimated growth-critical values of Ψ (Ψ_{crit}) for each species, with error bars showing 95% confidence intervals for the mean. Solid lines depict the fit of the negative exponential function by nonlinear least squares regression. The estimated growth-critical value of the HDI is indicated by the dashed vertical line. Species shown include Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco), ponderosa pine (*Pinus ponderosa* P. & C. Lawson), and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm).

Table 3 Parameter estimates for the relationship between water potential (Ψ) and the hydrometeorologic dryness index (HDI)

Species	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
Douglas-fir	Ψ_{max}	-0.465	0.048		
	k	0.068	0.008		
	Ψ_{crit}	0.911		-0.986	-0.832
Ponderosa pine	Ψ_{max}	-0.388	0.063		
	k	0.047	0.007		
	Ψ_{crit}	-0.734		-0.823	-0.642
Engelmann spruce	Ψ_{max}	-0.483	0.061		
	k	0.031	0.006		
	Ψ_{crit}	-0.706		-0.797	-0.613

Additionally, analyses of seasonally integrated records of HDI may prove useful for estimating inter-annual variation in growth for both modeling and the development of proxy climate records from tree rings. Of course, in practicality, tree growth is rarely limited by only one factor and interactions among these limiting factors may change seasonally.

If τHDI_{crit} were the sole factor controlling τSRI_{max} , we would expect $\tau\text{SRI}_{max}/\tau\text{HDI}_{crit}$ to equal 1: however, we see that the slope of this relationship is ≈ 0.76 based on all trees (Table 2). Several explanations for this result are plausible. For one, trees growing in the driest locations are likely to begin growth earliest

because these sites are also typically the warmest during the day, and temperature is probably the primary control on the initiation of growth in the cold spring climate of the Northern Rockies (Oribe *et al.*, 2003; Rossi *et al.*, 2008). As growth in these trees began as early as April, it is likely that low soil and air temperatures exerted considerable control over rates of radial growth, especially at night when Ψ conditions are most favorable for growth. In addition, those trees living in the wettest locations (such as those at the wettest site in 2014) did not regularly experience HDI_{crit} until late July. For these trees, other factors such as a decreasing photoperiod may begin to exert considerable control over growth rates later in the season (Rossi *et al.*, 2006b). It is likely that HDI imparts the greatest control over growth in trees when other factors such as temperature and photoperiod are not limiting. These moderate conditions typify growing conditions for trees at the intermediate wetness site, including western larch, where, although not statistically different from values for other groupings of trees given our level of replication, $\tau\text{SRI}_{max}/\tau\text{HDI}_{crit}$ most closely approached 1, at 0.98 and 1.03 for larch and intermediate site trees, respectively (Table 2).

It is also important to note that we aimed to quantify the seasonal evolution of a critical level of HDI (and associated Ψ) for growth limitation. As such, we based our analyses on low-pass filtered daily maxima (growth) and daily average (HDI) data. While these variables integrate the high-frequency variability of moisture conditions and stem radius dynamics over long time periods, they do not necessarily represent how the system behaves over short time steps. According to theory, growth probably occurs somewhat opportunistically when VPD and soil moisture facilitate high Ψ (e.g. at night-time), leading to alternating periods of growth and zero growth (Zweifel *et al.*, 2016), and it can be expected that such dynamics underlie the findings presented here.

Water potential (Ψ) controls on radial growth

While HDI_{crit} and τHDI_{crit} are strong predictors for peak tree growth, the mechanism by which these variables may influence growth is hypothesized to involve Ψ . The process by which Ψ directly limits growth has been suggested from laboratory results for some time (Boyer, 1970; Hsiao, 1973). However, to date there has been little research devoted to describing this process within actual forest communities or across a range of growing conditions. Steppe *et al.* (2006) used *Fagus sylvatica* to demonstrate the mechanics of radial tree stem growth as governed by the Lockhart equation (Lockhart, 1965), which describes the mechanical and hydraulic process of cell expansion. Similarly, Zweifel *et al.* (2016) provided evidence for threshold-type growth dynamics in multiple temperate forest tree species with their zero-growth model of stem radii. Both approaches considerably improved model simulations of growing stem radius dynamics, providing additional support for the role of Ψ in the radial growth of tree stems via its importance to the Lockhart model of cell expansion (Boyer *et al.*, 1985).

Our estimates of Ψ_{crit} (-0.71 to -0.91 MPa) were similar to values suggested by Körner (2015) to be critical for optimal meristem function (-0.5 to -0.8 MPa). However,

absolute values for Ψ estimated from branch-level water potential should be interpreted cautiously as some uncertainty results from the estimation of water potential gradients along the flow path from the bole to the branch. We estimated Ψ_{crit} and Ψ in general to be slightly lower in Douglas-fir trees than in ponderosa pine or Engelmann spruce, which is consistent with earlier findings that demonstrate lower vulnerability to cavitation in Douglas-fir than in ponderosa pine (Stout & Sala, 2003). In the studied watershed, Douglas-fir dominates stands and grows across a larger range of moisture conditions than other species, suggesting a competitive advantage. Furthermore, because Douglas-fir was able to maintain growth at lower Ψ than co-occurring species, it may be able to acquire more carbon via a lower degree of stomatal regulation without necessarily sacrificing growth in size.

The consistency of the growth response across environmental gradients and among different tree species

Synchrony in the growth response of different tree species to HDI_{crit} is somewhat counterintuitive given the general expectation that tree species are physiologically adapted for a particular moisture range. For example, within the North Fork Elk Creek watershed, ponderosa pine is almost entirely restricted to hot and dry landscape positions, while Engelmann spruce is generally restricted to wet and cool locations. However, despite growing in different moisture habitats, the level of HDI critical for sustained growth was similar for these two species. Additionally, the predictability of the growth response to HDI was consistent across multiple environmental gradients regardless of species (Table 2). This implies that, despite the expectation of different species-specific responses to water stress, the role of Ψ in cambial cell expansion may be well conserved, and acts as a unifying feature across a range of species.

The emergent properties of tree growth and water relations reflect an underlying set of important physiological trade-offs, balancing the need to acquire and store carbon, to protect hydraulic function, and to develop and expand new tissues. For trees in dry regions, these needs must be consistently met despite often challenging moisture conditions. While we do not yet fully understand the mechanistic details of how these needs are balanced, the moisture supply and demand framework (in this case HDI) can be a useful tool in predicting the outcomes of this balancing act where a reliable physiological response (such as growth limitation) exists (e.g. Sperry *et al.*, 2016). In the semi-arid system studied, growth was rapid in the short but well-watered conditions of spring; however, in the dry warm season, prioritization of carbon assimilation drove xylem tensions higher in transpiring trees. The tradeoff is sensible, as carbon for respiration and the maintenance of hydraulic function represents an immediate requirement for survival (Sevanto *et al.*, 2014). However, growth ultimately shapes a forest and its myriad ecological processes over time, and, as such, must remain a fundamental focus in our understanding of the relationship between climate and forest ecosystem function.

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Author contributions

J.M., J.H., K.J., N.L. and Z.H. designed the research. N.L. and J.H. collected the water potential data. J.M., N.L., K.J., J.H. and Z.H. developed the research site, participated in data collection and edited the manuscript. J.M. led the analysis and wrote the paper.

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