The influence of hydrological variability on inherent water use efficiency in forests of contrasting composition, age, and precipitation regimes in the Pacific Northwest

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A R T I C L E   I N F O

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A B S T R A C T

The Pacific Northwest (PNW) region of the United States has some of the most productive forests in the world. As precipitation regimes may shift with changing climate in this area, droughts are predicted to increase in both frequency and degree of severity, which will have a significant impact on already drought-prone ecosystems. When modeling ecosystem responses to drought, it is important to consider the physiology of individual tree species since the variations in drought sensitivity among species is easily overlooked when plants are characterized using broad plant functional types. Here we explore the use of inherent water-use efficiency as an index of drought sensitivity in semi-arid young and mature ponderosa pine forests and a mesic mature Douglas-fir forest in the PNW. Summer maximum of an evapotranspiration-based WUE (WUEi) was 2.5 times higher in young and mature pines in semi-arid climate than Douglas-fir in mesic climate (12.2 and 11.3 versus 4.7 g C kPa per kg H2O, respectively). In contrast, annually averaged WUE, was similar among the sites (2.8 g C kPa per kg H2O for pines and 2.4 g C kPa per kg H2O for Douglas-fir). The effect of drought stress on WUEi was most pronounced in young pine, followed by mature pine and Douglas-fir (32, 11, and 6% increase in WUE, per % decline in soil water content, respectively) which reflect differences in age-related ecosystem structure (root system, stem capacitance, and soil water holding capacity). Among sites, the responses of WUEi to climate variability were largely driven by changes in evapotranspiration (ET) compared to gross primary productivity (GPP). However, in areas where evaporation is the primary component of ET, such as the open canopy ponderosa forests of the PNW, the contribution of soil processes to ET can overshadow the reaction of vegetation transpiration (T) to changes in water availability. In these cases, utilizing a transpiration-based WUE (WUEi, T) in vegetation models will yield a more accurate representation of plant activity during drought. These results highlight the importance of incorporating differences in species- and age-related WUEi in models in diverse forest types at regional and global scales to improve predictions in ecosystem responses to climate change.

1. Introduction

Forest ecosystems are increasingly vulnerable to tree mortality as global climate change progresses (Allen et al., 2010; Williams et al., 2012). Rates of forest decline have particularly increased in regions where low levels of water availability are further exacerbated by a warming climate (Assal et al., 2016). Water limitations result in reductions in forest productivity (Jung et al., 2010; Thomas et al., 2009; Zha et al., 2010; Zhao and Running, 2010) and increases the susceptibility of trees to insects and disease (Meddens et al., 2012). This is of growing concern in the field of climate change research as the net global forest carbon sink lies primarily in temperate and boreal forests (Pan et al., 2011) which may be storing a large fraction (35% per year) of the carbon released from the consumption of fossil fuels (IPCC, 1995; Tans et al., 1990). While the relationship between water availability and forest productivity has been well established, the ability of process models to accurately predict the sensitivity of simulated carbon uptake to drought must be improved (Law et al., 2000; Leuzinger and Thomas, 2011; Zeppel et al., 2011).

Ecosystem-scale water use efficiency (WUE = GPP/ET; GPP is gross primary production and ET is evapotranspiration) is a key diagnostic parameter to examine the link between carbon and water cycles. The responses of WUE to fluctuating environmental conditions is often used to approximate the physiological adaptations of an ecosystem to a
changing climate (Beer et al., 2009; Keenan et al., 2013; Linderson et al., 2012; Lu and Zhuang, 2010; Tang et al., 2014). WUE is also effectively used as an indicator of ecosystem drought stress (Brümmer et al., 2012; Irvine et al., 2004; Thomas et al., 2009). Various models have addressed the interaction between carbon and water cycles using WUE, and bio-physiological processes have been incorporated in such models to quantify carbon and water fluxes simultaneously via estimations of stomatal regulation (Sellers et al., 1997; Sun et al., 2011; Tian et al., 2010). Assessments of model performance on simulating WUE are conducted by comparing flux measurements across plant functional types (PFTs; Schwalm et al., 2010; Tang et al., 2014). However, due to the limited availability of field observations in drought-prone ecosystems, the dynamics of WUE from models have rarely been validated in these climates (Williams et al., 2001). Better utilization of available data in drought-prone ecosystems will vastly improve our understanding of carbon and water coupling and the responses of these ecosystems to current and potential variations in climate (Schwalm et al., 2010).

There have been recent global synthesis efforts to assess spatial variability and trends of WUE across ecosystems (Beer et al., 2009; Huang et al., 2015; Jasechko et al., 2013; Keenan et al., 2013; Linderson et al., 2012; Tang et al., 2014). The concept of inherent WUE (WUEi = GPP/VPD/ET; VPD is vapor pressure deficit), first proposed by Beer et al. (2009), utilizes the relationship between GPP and VPD to account for the confounding effect of VPD on the separation of GPP and ET responses to changes in climate. Using eddy flux data over 40 sites across a range of PFTs and climate conditions, Beer et al. (2009) reported the dynamic ranges of WUEi. Although few sites were in dry regions, they observed an increase in WUE, with short-duration moderate drought. Keenan et al. (2013) also showed a substantial upward trend in WUE, in mesic temperate and boreal forests of the Northern Hemisphere over the past two decades using FLUXNET eddy covariance data from 21 sites, which was proposed to be the result of a strong CO2 fertilization effect. Most of the global syntheses focus on the changes of WUE, associated with different PFTs, but few examined WUEi in regions that regularly experience drought, like the western USA.

Drought-prone semi-arid ecosystems comprise nearly 18% of the earth’s land area (2.4 billion hectares) and have substantial carbon sequestration potential (Lal, 2004; Rotenberg and Yakir, 2010). There is a pressing need to scrutinize the response of WUE in water-limited environments where WUE is directly influenced by interannual variations in drought stress. In separate prior studies in the semi-arid forests of Oregon, we examined interannual variability in WUE or WUEi, in young and mature ponderosa pine forests and found that they generally increased as summer soil water deficit and VPD increased and were higher in more extreme drought years (Irvine et al., 2004; Ruehr et al., 2012; Thomas et al., 2009; Vickers et al., 2012). We found higher WUE in young than mature and old ponderosa pine (5.3, and 4 g C m⁻² mm⁻¹, respectively) when adjusted for leaf area index (LAI) differences (Irvine et al., 2004). Vickers et al. (2012) reported that WUE was ~70% larger in young pine (4 g C kPa per kg H₂O) than mature pine (2.6 g C kPa per kg H₂O) during the seasonal drought. This indicates that the younger trees are more susceptible to drought stress than the mature trees due to the higher relative sensitivity of canopy conductance to VPD and earlier water shortage during seasonal drought. WUE in mature ponderosa pine increased with drought stress during the growing season with no obvious differences between relatively dry or wet years (2002-2008), suggesting the mature ponderosa pine can adapt well to increasing drought stress (Thomas et al., 2009).

The aforementioned studies focused on ecosystem responses to drought stress by evaluating WUE or WUEi, both of which are derived from measurements of ET, at ponderosa pines in semi-arid sites. However, one of the limitations of WUEi, particularly in drought-prone open canopy forests, is that the responses of trees to water availability can be unclear since ET is dominated not by tree transpiration, but a combination of understory transpiration and evaporation from the forest floor during water-limited periods (Black and Kellibler, 1989). Throughout periods of drought, particularly in low LAI forests, WUEi (derived from tree transpiration (T), GPP/VPD/T) can be a better representation of drought stress in trees can be.

This study includes further years of data in the young and mature ponderosa pine forests in addition to a new mesic site occupied by Douglas-fir, all of which experience seasonal drought. Our objectives were to: (1) determine the response of WUE, and WUEi to drought stress between mature evergreen needleleaf forests growing in mesic and dry climates (mature ponderosa pine vs. mature Douglas-fir) and differences among stand ages in semi-arid climate conditions (young vs. mature ponderosa pines) and (2) assess the feasibility of defining species- or age-specific WUEi as a plant trait for improving models.

2. Materials and methods

The study was conducted in mature and young ponderosa pine in the semi-arid climate of Central Oregon, while Douglas-fir is in the mesic ecoregion of Western Oregon. All sites are part of the Ameriflux network (http://amerifluxornl.gov; Fig. A.1 in Supplementary materials). Both the mature and young ponderosa pine sites are within the network’s Metolius site cluster that encompass a range of tree developmental stages since disturbance. The mature ponderosa pine forest (Ameriflux site US-Me2, referred to hereafter as MP) is located east of the Cascade Range crest near Sisters, Oregon USA at an elevation of 1255 m (44.452N, 121.557W; Table 1). The mean stand age is 64 years with the oldest trees aged about 100 years. The overstory is almost exclusively composed of ponderosa pine (Pinus ponderosa Dougl. ex Laws) with a few scattered incense cedars (Calocedrus decurrens (Torr.) Florin) and has a summer maximum leaf area index (LAI) of 2.8.

Table 1 Site characteristics at mature ponderosa pine (MP), young ponderosa pine (YP), and mature Douglas fir (DF) locations. Numbers in parenthesis indicate the measurement year.

<table>
<thead>
<tr>
<th>Site</th>
<th>MP</th>
<th>YP</th>
<th>DF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude (°N)</td>
<td>44.451</td>
<td>44.315</td>
<td>44.6465</td>
</tr>
<tr>
<td>Longitude (°W)</td>
<td>121.558</td>
<td>121.6078</td>
<td>123.5515</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>1255</td>
<td>1088</td>
<td>263</td>
</tr>
<tr>
<td>Diameter at breast height (cm)</td>
<td>32.3 (2011)</td>
<td>8.3 (2007)</td>
<td>32.1 (2006)</td>
</tr>
<tr>
<td></td>
<td>Rooting depth (m) 1.5</td>
<td>0.5</td>
<td>1.0</td>
</tr>
<tr>
<td></td>
<td>Soil depth (m) 1.5</td>
<td>0.5</td>
<td>1.0</td>
</tr>
<tr>
<td></td>
<td>Soil sand/silt/clay fraction (%)</td>
<td>sandy</td>
<td>loamy sand</td>
</tr>
<tr>
<td>30-year mean° annual temperature (°C)</td>
<td>5.7</td>
<td>7.6</td>
<td>10.6</td>
</tr>
<tr>
<td>30-year mean° annual precipitation (mm)</td>
<td>536</td>
<td>500</td>
<td>1821</td>
</tr>
</tbody>
</table>

° Soil C:N ratio at MP and DF was averaged from the measurements at 0–20, 20–50, and 50–100 cm depths.
° The 30-year mean (1981–2010) was obtained from the PRISM Group at Oregon State University (http://prismmap.nace.org/n/)
Tree height is homogeneous at about 17 m and the mean tree density is 325 trees ha\(^{-1}\) (Irvine et al., 2008). The understory is sparse with LAI of 0.6 and primarily composed of bitterbrush (\textit{Purshia tridentata} (\textit{Push}) \textit{Festuca idahoensis}) and greenleaf manzanita (\textit{Arctostaphylos patula} Greene). Soils at the site are sandy and freely draining with a soil depth of approximately 1.5 m (Schwarz et al., 2004; Irvine et al., 2008).

The young ponderosa pine forest (Ameriflux site US-Me3) was studied in a 16-year-old ponderosa pine plantation at an elevation of 1005 m (44.3154 N, 121.6078 W; Table 1) and located ~16 km south of MP. The site was clear-cut, stripped of debris, tilled, and replanted with clonal trees in 1987. The overstory is composed of ponderosa pine (\textit{Pinus ponderosa} Doug., \textit{Law}) and the understory is primarily Idaho bunchgrass (\textit{Pseudotsuga menziesii} (\textit{Mirb.}) Franco) and the maximum LAI is 9.4 as of 2006 (Thomas et al., 2013). Tree height is homogeneous at ~34 m, and the mean stand density is 414 trees ha\(^{-1}\). The understory is sparse and composed mainly of salal (\textit{Gaultheria shallon}) with a plant height of up to 0.8 m. Soils at the site are silty clay loam, well drained, and highly fertile. Deeper soils with more organic matter and clay results in a larger soil water holding capacity compared to pine sites.

The general climate in the region is characterized by hot, dry summers and precipitation that primarily occurs in winter and spring as a combination of snow and rain. DF experiences milder winters with little snow such that the growing season is almost year-round, whereas MP and YP experience snow and long periods of freezing temperatures with less total annual precipitation. Data used in these analyses include 2003–2012 for mature ponderosa pine, 2005–2008 for young ponderosa pine, and 2007–2010 for mature Douglas-fir. The 30-year mean temperature and precipitation, which were calculated using data from the Parameter-Elevation Regressions on Independent Slopes Model (PRISM Climate Group, Oregon State University, \textit{http://prism.oregonstate.edu}, 1981–2010), were 7.5 °C and 536 mm at MP, 7.6 °C and 500 mm at YP, and 10.6 °C and 1821 mm at DF (Table 1).

### 2.2. Eddy covariance and meteorological measurements

Eddy-covariance (EC) measurements at MP were conducted using a three-dimensional sonic anemometer (model CSAT3, Campbell Scientific Inc., Logan, UT, USA) and an open-path infrared gas analyzer (model LI-7700, LI-COR Inc., Lincoln, NE, USA) at an elevation of 1005 m (44.3154 N, 121.6078 W). The seasonal maximum LAI was 1.8 in 2007. Approximately 22% of the maximum LAI is that of understory, and the bunchgrass seneches in June. Soils are a freely draining sandy loam derived from volcanic ash (soil depth < 1 m).

The Douglas-fir forest (Ameriflux site US-MRf, referred to hereafter as DF) is located on the east side of the Coast Range of Oregon, USA at an elevation of 1005 m (44.646. N, 123.551.W). The average stand age is 58 years. The overstory is almost exclusively composed of Douglas-fir (\textit{Pseudotsuga menziesii} (\textit{Mirb.}) Franco) and the maximum LAI is 9.4 as of 2006 (Thomas et al., 2013). Tree height is homogeneous at ~34 m, and the mean stand density is 414 trees ha\(^{-1}\). The understory is sparse and composed mainly of salal (\textit{Gaultheria shallon}) with a plant height of up to 0.8 m. Soils at the site are silty clay loam, well drained, and highly fertile. Deeper soils with more organic matter and clay results in a larger soil water holding capacity compared to pine sites.

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Sap flux was measured by the heat dissipation technique (Granier, 1987) between April and November over a 10-year period at MP (2003–2012) and a 4-year period at DF (2006–2009). A detailed description of our sap flow measurement methods can be found in Irvine et al. (2002). In brief, sap flux sensors were installed across a range of tree sizes (diameter at breast height (DBH) from 22 to 41 cm in 12 trees at MP and from 29 to 48 cm in 10 trees at DF) based on a stand surveys to investigate variation in sap flux in relation to tree size and to accurately scale stand-level T. The selected trees were within the tower footprint at both sites. Sap flow was measured over the outer 20 mm of sapwood and recorded as a 10-min average of one-minute measurements (model CR10X, Campbell Scientific Inc.). Sap velocity was...
calculated empirically from probe temperature differentials (Granier, 1987) and zero flow was estimated at night when VPD ≤ 0.3 kPa. We also accounted for the proportion of sapwood area at different sapwood depths and the decline in sap velocity with sapwood depth when calculating tree transpiration. To measure the change in sap velocity with depth, in addition to the 20 mm sap flux probe, three 10-mm probes were installed at different sapwood depths in four trees at both the MP and DF sites. The decline in sap velocity with depth was calculated from mean daily sap fluxes from the profiles expressed relative to the sap flux over the 0–20 mm sapwood depth. Transpiration was estimated based on mean sap flux for each tree, the proportion of sapwood area at different sapwood depths, and the decline in sap flux with sapwood depth. The naturally occurring temperature gradient between the heater and reference probe is often a sizable source of error in sap flux measurement. This temperature gradient was assessed at the 0–20 mm sapwood depth in all trees. Errors associated with temperature gradients were 12% overestimation of mean daily sap flux at MP and DF and were corrected accordingly. In order to compare T and ET at the stand level, we scaled T by multiplying mean sap flux by sapwood-to-ground area ratio, derived from four inventory plots (each with a 15 m radius) located within the footprint of the EC system (see Irvine et al. (2002, 2004) for more detailed information).

At YP, sap flux was not measured during the EC measurement period. However, a similar young ponderosa pine site was established in 2010 (Ameriflux site US-Me6) and is located approximately 850 m north of YP. Both sites were re-forested in the early 1990s and had similarly aged ponderosa pines. At US-Me6, sap flux measurements were conducted for four trees from May through October in 2010 and 2011, using the methods described above (Ruehr et al., 2012). Errors associated with temperature gradients were 7% overestimation at YP and were corrected accordingly. Sapwood-to-ground area ratio for stand-level T was derived from tree inventories of 4 × 17 m radius plots. Given the fact that both sites contain the same species of similar age and are in close proximity to one another, we assumed a similar monthly ratio of T to ET between the two sites. We applied the ratio of T/ET at US-Me6 to estimate T at YP. We used YP as the site of interest to represent a young ponderosa pine because YP had more years of overlapping measurements with MP and DF than US-Me6.

2.4. Ecosystem processes and drivers

To diagrammatically interpret the dependency of WUE, on vegetation type and environmental conditions, canopy conductance (Gc) was calculated by rearranging the Penman-Monteith equation as follows:

$$Gc = \frac{k \cdot \Delta \cdot VPD}{\gamma \cdot \alpha} + \left(\frac{1}{\alpha} \cdot \left(\frac{Rn - G}{\lambda E} - 1\right)\right)^{-1}$$

(1)

where $\Delta$ is the slope of saturation vapor pressure curve (kPa K$^{-1}$); $\lambda$ is the psychrometric constant (kPa K$^{-1}$); $E$ is evaporation; $\rho$ is air density (kg m$^{-3}$); $c_p$ is the specific heat of air (MJ kg$^{-1}$ K$^{-1}$); $Rn$ is net radiation (W m$^{-2}$); $G$ is ground heat flux (W m$^{-2}$); VPD is vapor pressure deficit (kPa); and $g_a$ is the aerodynamic conductance (m s$^{-1}$). Levels of $g_a$ are estimated as:

$$g_a = \frac{1}{k_e} = \frac{1}{k_{aw} + n}$$

(2a)

$$\alpha = \frac{\Delta}{\Delta + \gamma}$$

(2b)

$$k_e = \frac{\Delta}{\gamma}$$

(2c)

where $g_a$ is the aerodynamic resistance (s m$^{-1}$) which consists of the aerodynamic resistance of momentum transfer ($r_m$) and the excess resistance ($r_s$; Thom, 1972; Kim and Verma, 1990); $\Delta$ is mean horizontal wind speed at a height; $u$ is the friction velocity; $k$ is the Karman’s constant; $K$ is the thermal diffusivity; and $D_o$ is the molecular diffusivity of water vapor. Stomatal conductance at canopy-level ($g_s$) was calculated by substituting $T$ from sap flux measurements for $\lambda E$ in Eq. (1).

We computed a monthly time series of standardized precipitation evapotranspiration indices (SPEI) as a site-specific drought indicator (Vicente-Serrano et al., 2013, 2010). SPEI is calculated as a function of $D$ (the difference between precipitation and potential ET, $ET_p$), and then aggregated at different time scales to represent the cumulative water balance over the previous number of months as follows:

$$D_k^f = \sum_{i=0}^{k-1} (R_{p,i} - ET_{p,i}) \quad n \geq k$$

(3)

where $k$ (in months) is the timescale of aggregation and $n$ is the calculation number. We used the SPEI package (Beguería and Vicente-Serrano, 2013) in R (R Core Team, 2016) and a 6-month integration period ($k$) to calculate SPEI. We estimated $ET_p$ using the following equation:

$$ET_p = \alpha_{PT} \frac{\Delta R_{p}}{\rho \left(\Delta + \gamma\right)}$$

(4)

where $\alpha_{PT}$ is the Priestley-Taylor coefficient (=1.26; Priestley and Taylor, 1972). A positive SPEI indicates wet conditions, whereas negative SPEI indicates dry conditions.

Half-hourly values of WUE were calculated during the daytime (defined as when PAR exceeded 150 μmol m$^{-2}$ s$^{-1}$). WUE was derived from ET, which was converted from $\lambda E$ (latent heat flux, W m$^{-2}$). To calculate WUE, $T$, levels of T were normalized by LAI to determine stress per unit leaf area. In order to dampen the influence of precipitation on WUE, we excluded data both during and for 6 h after precipitation events. In addition, the pumice was permeable at the sites, leading to a very quick percolation after precipitation. The top soil layer was never saturated and this minimized bare soil evaporation. In order to focus on flux dynamics in response to drought, we calculated a relative fraction of each variable as the ratio of the values under non-limited soil water conditions (pre-drought) to those under limited soil water condition (drought). For the analysis, we selected data (PAR > 500 μmol m$^{-2}$ s$^{-1}$) for the non-limited soil condition with the highest plant activity from DOY 157–166 for MP and YP and DOY 166–175 for DF.

Pronounced seasonality in water availability results in dynamic ecosystem carbon and water cycles at the sites. To examine ecologically meaningful events associated with the site hydrology, we present annual variations in precipitation and WUE, based on the water year (1 October–30 September). We used anomalies in precipitation intensity and annual precipitation amount to define dry, normal, and wet years (U.S. Geological Survey, 1991). Precipitation intensity was calculated as annual precipitation divided by total number of precipitation days per year. Anomalies were defined as deviates from the mean precipitation intensity and annual precipitation during the measurement years. We defined a year as “dry” when both intensity and amount were below the normal values (i.e. negative) in a given year and “wet” when both parameters were greater than the normal values (i.e. positive). This analysis was applied only to MP where interannual variability of WUE, can be assessed due to the length of the measurement period.

2.5. Statistical analyses

Subset regression analysis was employed to determine explanatory variables of variation in WUE, using R package leaps (Lumley, 2017). The analysis assessed all possible models using a specified set of variables. The variables that best satisfied model-fitting criterion were identified based on Bayesian information criterion (BIC). We calculated $\Delta$(BIC) ($=\text{BIC}_{i} - \text{BIC}_{\text{min}}$) and applied a weight method to quantify the
relative importance of each variable (Burnham and Anderson, 1998). The weight of each model was calculated as follows:

$$w_i(BIC) = \frac{\exp\left(-\frac{1}{2} \Delta_i(BIC)\right)}{\sum_{i=1}^{k} \exp\left(-\frac{1}{2} \Delta_i(BIC)\right)}$$

(5)

where $\Delta_i(BIC)$ is the distance from various models to the best model (in this case, the smallest BIC). If the sum of $w_i(BIC)$ of a variable is larger, relative to other variables, then the variable was regarded to be more important. We considered only linear models for the subset models and used data from those months which played a dominant role in seasonal variation of WUEi (May–October) for each year in the analysis. We selected air temperature ($T_{air}$), soil water content (SWC), water balance (P–ET), and shortwave radiation ($R_s$) as explanatory variables. We used water balance as one of the water-related drivers as it is more critical than precipitation for plant physiological processes.

To assess differences among means of the annual WUEi, we conducted Tukey-Kramer pairwise multiple comparison tests (Matlab Version 8.2.0.701 (R2013b), The MathWorks Inc., Natick, MA, 2013). Prior to the Tukey-Kramer comparison, we conducted Kruskal-Wallis ANOVA function test. When the null hypothesis, which states that all means are equal, was rejected, we proceeded with the Tukey-Kramer ANOVA function test. If the sum of $w_i(BIC)$ of a variable is larger, relative to other variables, then the variable was regarded to be more important. We considered only linear models for the subset models and used data from those months which played a dominant role in seasonal variation of WUEi (May–October) for each year in the analysis. We selected air temperature ($T_{air}$), soil water content (SWC), water balance (P–ET), and shortwave radiation ($R_s$) as explanatory variables. We used water balance as one of the water-related drivers as it is more critical than precipitation for plant physiological processes.

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lowest but the seasonal variations in WUEi were much larger at the pine sites than Douglas-fir (Fig. 1, Table 2). Values of WUEi ranged from 0.4 to 12.2 g C kPa per kg H2O at YP and 0.3 to 11.3 g C kPa per kg H2O at MP over the entire measurement period for each site. WUEi was higher at YP than MP when site-specific drought was more severe at YP (summers of 2006 and 2008) (Fig. A.3 in Supplementary materials). Outside of the seasonal drought period, MP and YP had similar monthly WUEi, suggesting a species-specific WUEi under non-water limiting conditions (Vickers et al., 2012). Although monthly WUEi was higher at the pine sites than Douglas-fir in summer, the minimum WUEi at the Douglas-fir site (0.7 g C kPa per kg H2O) was roughly twice that of the pine while the maximum Douglas-fir WUEi (6.2 g C kPa per kg H2O) was less than half that of the pine sites (Table 2). Despite seasonal variations in WUEi among years and sites, annual average WUEi was similar across sites with values of 2.8 ± 0.6 g C kPa per kg H2O for MP and YP and 2.4 ± 0.2 g C kPa per kg H2O for DF.

The range in monthly values of WUEi_T was greater in ponderosa pine (3.7–26.2 g C kPa per kg H2O at YP and 1.5–16.1 g C kPa per kg H2O at MP) than Douglas-fir (0.9–4.5 g C kPa per kg H2O; Table 2). Unlike patterns in WUEi, values of annual WUEi_T varied by both species and age and were highest in YP, followed by MP and DF (12.0, 6.2, and 1.4 g C kPa per kg H2O, respectively). Levels of annual WUEi_T were greater than WUEi by ~430% at YP and ~220% at MP, whereas WUEi_T was only 58% of WUEi at DF.

In order to examine the influence of physiological differences in species and age on WUEi_T, we compared GPP, T and WUEi_T (all normalized per unit leaf area; Fig. 2). Normalized GPP, T, and WUEi_T were averaged from June to September of 2007–2009, during which T was available at all sites. In ponderosa pine, WUEi_T increased substantially as summer soil water deficit increased, but showed almost no changes in Douglas-fir. The seasonal variation in normalized GPP and T was much larger at the two pine sites than at Douglas-fir. Compared to the maxima in June, normalized GPP and T were reduced by 40 and 80% in September at MP, 70 and 80% at YP, and 21 and 26% in DF. Higher rates of decline suggest more seasonal drought water stress in ponderosa pine than in Douglas-fir. The effect of drought stress on normalized GPP, T, and WUEi_T was more pronounced in YP than MP.

3.3. Explanatory variables of WUEi and WUEi_T

Environmental drivers of WUEi varied between sites. The most important drivers of WUEi at MP were Tair, SWC, P-ET, and Rg, whereas SWC was substantially more important than other variables at YP (Table A.2 in Supplementary materials). At DF, Tair was more important than water-related drivers. Given the close correlation between Tair and VPD (Y = 0.205e0.12X, R² = 0.92 at MP, and Y = 0.08e0.13X, R² = 0.77 at DF, where X = Tair and Y = VPD), the dependence of WUEi on Tair infers that VPD actually governs patterns of WUEi.

To explore ecosystem responses to VPD, we examined the trends in WUEi and WUEi_T with varying VPD under both limited and non-limited soil water conditions (Fig. 3). When soil water was not a limiting factor, WUEi increased with VPD at all sites. The rate of increase was similar at the two pine sites but steeper at the Douglas-fir site, indicating a higher sensitivity of WUEi to changes in VPD at the Douglas-fir site. The responsiveness of WUEi to changes in VPD under limited soil water conditions increased markedly at MP and YP at low to medium values of VPD, but tended to level off or even decrease as VPD continued to increase. At DF, however, the rate of WUEi response to changes in VPD under water-limited conditions seemed to be less affected by levels of SWC, showing patterns that were similar to those of a non-water limited system.

The responses of WUEi_T to changes in VPD were very similar to those of WUEi, showing substantial increases of WUEi_T at the two pine sites and almost no change of WUEi_T at the Douglas-fir when soil water...
increases in WUE\textsubscript{i,T} per\% decline in SWC at MP, YP, and DF, respectively; Fig. 4C). Levels of \(g_s\) were lowered by 78\% in mature pine, 73\% in young pine, and 27\% in Douglas-fir (Fig. 5B). Young pine had the lowest \(G_c\) (1.3 mm s\(^{-1}\)) and \(g_s\) (0.3 mm s\(^{-1}\)), which were \(\sim\)45\% of mature pine and \(\sim\)20\% of Douglas-fir.

### 3.4. Interannual variation of WUE\textsubscript{i} at the mature pine site

Interannual variability of WUE\textsubscript{i} was examined only at the MP site due to the length of the measurement period. WUE\textsubscript{i} was highly dependent on amounts of precipitation, showing higher annual means (3.7 g C kPa per kg H\(_2\)O) during drought years (2003–2005) and lower (2.0 g C kPa per kg H\(_2\)O) during wet years (2010–2011, \(p < 0.001\), Fig. 6A). Degrees of the identified drought and wet years were within the range of the 30-year time window (1981–2010; data not shown). The drought in 2003 corresponded with the lowest annual mean GPP, which significantly differed from GPP in the other years (Fig. 6B). However, the annual means of GPP in other drought years (2004 and 2005) were similar to those among non-drought years. The annual sum of GPP was 30\% lower in 2003 compared to the measurement period maximum observed in 2012 (1830 g C m\(^{-2}\) yr\(^{-1}\)) but < 10\% lower than GPP in the drought years of 2004 and 2005 (Table 2). The annual mean of ET in drought years was significantly lower than in wet years (Fig. 6C). The interannual daily mean of ET gradually increased from 1.1 to 1.9 mm d\(^{-1}\) (410.0–686.5 mm of annual ET) as drought stress was relieved by increasing annual amounts of precipitation.

The difference between annual WUE\textsubscript{i} and the average WUE\textsubscript{i} over the measurement period (WUE\textsubscript{i} anomaly, \(\Delta\text{WUE}\textsubscript{i}\)) at MP decreased by

shifted from non-limited to limited conditions. Unlike the similar response of WUE\textsubscript{i} to VPD at the two pines under water-limited conditions, a higher sensitivity of WUE\textsubscript{i,T} to VPD was observed in young pine than mature pine. These results suggest that reduced SWC enhanced the influence of VPD on WUE\textsubscript{i} and WUE\textsubscript{i,T} at MP and YP but not at DF.

To more closely examine the relationships between WUE\textsubscript{i} and SWC and between WUE\textsubscript{i,T} and SWC, we compared trends in WUE\textsubscript{i} and WUE\textsubscript{i,T} during drought and non-drought conditions (expressed as a relative fraction and changes in SWC; Fig. 4). As SWC declined during the summer, WUE\textsubscript{i} increased by 3.2 times at MP, 3.5 times at YP, and 4\% at DF relative to pre-drought conditions (Fig. 4D). The rates of WUE\textsubscript{i} increase in response to declining SWC were greater in ponderosa than in Douglas-fir, confirming that SWC was a more important driver of WUE\textsubscript{i} in the more water-limited pine forests compared to the mesic Douglas-fir forest (Table A.2 in Supplementary materials & Fig. 4). As SWC approached minimum values, the relative fraction of ET was more sensitive to changing SWC than that of GPP at all sites (Fig. 4A–C). In order to examine plant response to SWC, the responses of WUE\textsubscript{i,T} to SWC were also tested. The results were very similar to those of WUE\textsubscript{i} with the largest rates of change of WUE\textsubscript{i,T} in young pine, followed by mature pine and Douglas-fir (12, 27, and 9\% increases in WUE\textsubscript{i,T} per\% decline in SWC at MP, YP, and DF, respectively; Fig. 4E–H).

The increases in WUE\textsubscript{i} and WUE\textsubscript{i,T} in response to changes in SWC were strongly associated with the decreases in conductivity (\(G_c\) for WUE\textsubscript{i} and \(g_s\) for WUE\textsubscript{i,T}). Compared to \(G_c\) and \(g_s\) observed during non-drought conditions, \(G_c\) was reduced by 69\% in mature pine, 76\% in young pine, and 10\% in Douglas-fir when SWC reached its minimum (10\% at US-Me2, 6\% at US-Me3, and 20\% at US-MRf; Fig. 5A). Levels of \(g_s\) were lowered by 78\% in mature pine, 73\% in young pine, and 27\% in Douglas-fir (Fig. 5B). Young pine had the lowest \(G_c\) (1.3 mm s\(^{-1}\)) and \(g_s\) (0.3 mm s\(^{-1}\)), which were \(\sim\)45\% of mature pine and \(\sim\)20\% of Douglas-fir.

![Fig. 3. Relationships between vapor pressure deficit (VPD) and inherent water use efficiency (WUE\textsubscript{i}) calculated with evapotranspiration (ET) (panels A and B) and between VPD and inherent water use efficiency (WUE\textsubscript{i,T}) calculated with transpiration (T) (panels C and D) under non-limited and limited soil water conditions at mature ponderosa pine (MP), young ponderosa pine (YP), and mature Douglas-fir (DF) sites. WUE\textsubscript{i} and WUE\textsubscript{i,T} were biased every 0.3 kPa VPD using half-hourly daytime data (PAR > 500 \(\mu\)mol m\(^{-2}\) s\(^{-1}\)). Data for non-limited soil water conditions were selected when the standardized precipitation evapotranspiration index (SPEI) > 0 and soil water content (SWC) > SWC\textsubscript{ave} at each site, whereas criteria defining limited soil water were when SPEI < 0 and SWC < SWC\textsubscript{ave}. SWC\textsubscript{ave} and SWC\textsubscript{ave} were 22 and 10\% at MP, 12 and 6\% at YP, and 29 and 20\% at DF. Error bars indicate standard errors.](image-url)
Fig. 4. Relationships between soil water content (SWC) and gross primary productivity (GPP), evapotranspiration (ET), transpiration (T), vapor pressure deficit (VPD), inherent water-use efficiency from ET (WUE_i), and inherent water-use efficiency from T (WUE_i_T) during summers for mature ponderosa pine (MP, panels A and E), young ponderosa pine (YP, panels B and F), and mature Douglas-fir (DF, panels C and G). Each variable is presented as a fraction relative to pre-drought conditions. The relationship between SWC and WUE_i for each site (panel D) are described by the following linear regressions: $y = -0.11x + 3.71$, $R^2 = 0.68$ at MP, $y = -0.32x + 4.72$, $R^2 = 0.52$ at YP, and $y = -0.04x + 2.32$, $R^2 = 0.38$ at DF. The relationship between SWC and WUE_i_T for each site (panel H) are: $y = -0.12x + 3.50$, $R^2 = 0.79$ at MP, $y = -0.27x + 3.88$, $R^2 = 0.30$ at YP, and $y = -0.09x + 3.69$, $R^2 = 0.56$ at DF. Values next to the regression lines represent the slope of the regression.

Fig. 5. Values of (A) canopy conductance ($G_c$) and (B) stomatal conductance ($g_s$) under non-limited and limited soil water conditions at mature ponderosa pine (MP), young ponderosa pine (YP), and mature Douglas-fir (DF) sites. Daytime data (PAR > 500 μmol m$^{-2}$ s$^{-1}$) were selected in the analysis from the data collected during the measurement years. Error bar indicates standard deviation.
0.13 g C kPa per kg H₂O per year (p < 0.05; Fig. 7A). A positive trend in the ET anomaly (ΔET) was observed (29 mm yr⁻¹ with p < 0.001), whereas the GPP anomaly (ΔGPP) showed absence of an annual trend (slope of 26 g C yr⁻¹ with p = 0.21), suggesting ΔWUE was more strongly affected by changes in ΔET and not the changes in ΔGPP.

The dependence of annual WUE on the timing and quantity of precipitation was assessed by comparing two drought years with different precipitation distributions: a wetter summer in 2004 (58 mm of precipitation over 15 rain events between August and September) and a drier summer in 2005 (< 2 mm with one rain event between August and September, Fig. 8). Compared to the average WUE, (6.6 g C kPa per kg H₂O) in the two months over the 10-year period, WUE decreased by 30% in 2004 (4.4 g C kPa per kg H₂O) and increased by 42% in 2005 (9.3 g C kPa per kg H₂O). WUE in 2004 was only half that of in 2005 in these months that showed the most contrasting precipitation patterns. There were more periods of a higher ratio (T/ET) in 2004 compared to the prolonged dry period in 2005, resulting in a lower WUE_T in 2004 than 2005. In 2005, prolonged dryness led to a decrease in the ratio of T to ET primarily due to an extremely low T (< 0.2 mm) which resulted in a substantial increase in WUE_T beginning in mid-August. As found in an experiment by Ruehr et al. (2012), the increase in WUE after August was because gs declined more than photosynthesis. The VPD-induced response of gs was strongly affected by soil water availability, which affected T more than ET.

To examine the prolonged influence of changing seasonal water availability on interannual WUE, we carried out a correlation analysis between annual WUE, and aggregated monthly water balance over the preceding 24 months (Fig. A.4 in Supplementary materials). Annual WUE, exhibited a strong negative correlation (−0.9 < r < −0.5, p < 0.05) with water balance in October when summer drought was alleviated by intensive rains as well as in March at the onset of the wet season. However, the influence of these events on the overall water balance was significant only for a short duration (1–2 months). During the summer drought in July and August, a strong positive correlation was found and the effects persisted for up to 5 months (0.6 < r < 0.9, p < 0.05). We found no evidence that the effects of seasonal drought had an interannual effect on the water balance at the site.

4. Discussion

4.1. Influence of environment on WUE_T in mature stands

We compared WUE, and WUE_T among species within the evergreen plant functional type in mesic (Douglas-fir) and seasonally water-limited (ponderosa pine) ecoregions. The average annual WUE, in the overlap years of 2007–2010 was nearly identical for the two stands (2.6 and 2.7 g C kPa per kg H₂O for DF and MP respectively; Fig. 1, Table 2). Although no studies were found that specifically measured WUE, for
mature ponderosa pine, values for DF and MP were within the range reported by Beer et al. (2009) for evergreen needle-leaved forests which included Douglas-fir, Scots pine, and spruce forests (1.6–3.5 g C kPa per kg H$_2$O). The average annual WUE$_{i_T}$ in the overlap years of 2007–2009 was greater by roughly 4.0 times in MP (6.2 g C kPa per kg H$_2$O) compared to DF (1.4 g C kPa per kg H$_2$O; Table 2), suggesting differences in the physiological responses of plant functional types to soil water availability and climate (Fig. 2).

Soil water content and atmospheric demand played critical roles in driving WUE, and WUE$_{i_T}$ in MP, whereas trends for DF were almost entirely dependent on atmospheric demand (Figs. 2–4). These results indicate that future changes in the magnitude of VPD due to climate warming will have a significant impact on ecosystem water use (Novick et al., 2016). However, because soil water is still a major factor, and is hyperbolically related to ET, even small changes in soil water will also have large effects on ecosystem WUE (Jung et al., 2010). However, our current predictions of how future patterns in precipitation (and therefore soil moisture) will be altered are uncertain (Burke and Brown, 2008). In drier regions, like those included in this study, soil moisture reserves are depleted rapidly during the summer growing season which have a significant effect on canopy and stomatal conductance (and thus WUE, and WUE$_{i_T}$) in these ecosystems (Hubbard et al., 2010) and may be exacerbated by future changes in climate.

The higher sensitivity of WUE, and WUE$_{i_T}$ to changes in soil water content that were observed in MP can be explained by a larger reduction in both canopy, $G_c$, and stomatal, $g_s$, conductance when compared to DF (Fig. 5). Ponderosa pine is more vulnerable to cavitation than Douglas-fir but is considered more drought tolerant (Minore, 1979). Ponderosa pine offsets this vulnerability through functional (more sensitive stomatal closure) and structural (increased sapwood) drought avoidance mechanisms (Stout and Sala, 2003). The pine exhibits greater stomatal sensitivity to stress because of the increased susceptibility of roots to cavitation, which, as drought stress occurs, limits water transport and quickly signals stomatal closure (Alder et al., 1996). Ponderosa pine also shifts biomass allocation from needles to sapwood, thereby increasing water storage and maximizing leaf-area-based water transport even under stress (DeLucia et al., 2000). This adaptation results in the lower GPP and decreased levels of ET that were observed in this study (Fig. 4). Rates of ET decline were greater than those of GPP reduction at both sites and ET decreased more in MP (2.7–0.9 mm d$^{-1}$) than DF (2.2–1.6 mm d$^{-1}$) likely reflecting the physiological adaptations of pine to drought. In addition, the contribution of T to ET lessened with soil water depletion, changing from 40 to 30% in MP and from 62 to 40% in DF (data not shown). Lower ratios of T to ET suggest that, under drought stress, changes in ET were mostly due to changes in E, which compensated for the reduced contribution of T from plants to total ecosystem water loss at both sites (Fig. 2).

Humphreys et al. (2003) reported that Douglas-fir showed a higher decline in canopy conductance under very low SWC (< 10%) than under high SWC at a given VPD. In our study, however, higher stomatal closure occurred only on individually isolated hot days (data not shown), which corresponded with high daily maximum water demand that could cause supply velocities through the xylem to become limiting in late summer (VPD > 1.2 kPa; 4% of the total data within the 4-year measurement period). In addition to a relatively higher minimum SWC (20%; Fig. A.2 in Supplementary materials) compared to the sites in Humphreys et al. (2003), sporadic rain events ranging from 2 to 12 days per month in summer caused a transient partial recovery of SWC, leading lesser degree of drought stress to soil water deficit in our sites.

4.2. Influence of stand age on WUE$_i$ and WUE$_{i_T}$

We found that young and mature pines responded differently to water limitations. The effect of drought stress on WUE$_i$ was more pronounced in young pine than mature pine (Fig. 4D). More severe drought stress in young pine may be due to a lower baseline in soil water content, lesser stem capacitance, and a shallower rooting depth when compared to mature pine. Irvine et al. (2004) reported that a young ponderosa pine extracted 80% of water from a depth of 80 cm or less, whereas a mature ponderosa pine extracted 50% from below 80 cm during summer months. We speculate that shallow root depth at the YP site limited an access to water in deeper soil layers, resulting in lower $G_c$ (1.3 mm s$^{-1}$; Fig. 5A) and higher sensitivity of WUE$_i$ (Fig. 4D) to soil water content at that site. In addition, the relatively lower LAI at the YP site could result in a higher ratio of E to T during non-limited water periods due the increased amounts of radiation reaching the soil surface. When drought occurs, rates of E may be lowered significantly yielding a much higher value of WUE$_i$ (Vickers et al., 2012).

When WUE$_{i_T}$ was examined as an indicator of whole plant responses to drought at the two pine sites, WUE$_{i_T}$ was 27.2 g C kPa per kg H$_2$O at the young pine and 10.0 g C kPa per kg H$_2$O at the mature pine under soil water limited conditions, which were 2.8 and 1.7 times larger than WUE$_i$, respectively. The higher values of WUE$_{i_T}$ observed in young pine were the result of increased stomatal down-regulation coupled with substantially lowered rates of T (Figs. 2, 4, and 5; Irvine et al., 2004; Law et al., 2000). At the tree level, $g_s$ alters T in order to minimize loss of hydraulic system function (Brooks et al., 2002). Young ponderosa pine have lower hydraulic resistance than mature ponderosa pine, resulting in hydraulic system failure through xylem cavitation and...
greater restriction in gs during severe drought periods (Law et al., 2000). In this study, as soil water deficit increased in late summer, values of gs at the YP site were less than half those observed at the MP (0.3 and 0.7 mm s\(^{-1}\) for YP and MP, respectively; Fig. 4B) as a result of lower T rates (0.3 and 0.5 mm d\(^{-1}\) for YP and MP, respectively; data not shown).

4.3. Influence of interannual variation in precipitation on mature pine WUE\(_i\)

The variation in annual WUE\(_i\) in mature ponderosa pine was tightly linked with annual amounts and timing of precipitation. The measurement period at the MP site began with three extremely dry years (2003–2005) and ended with two wet years (2011–2012) which had a significant effect on ET and contributed to the observed decline in ∆WUE\(_i\) (−0.13 g C kPa per kg H\(_2\)O; Fig. 7). Keenan et al. (2013) found the opposite (an increasing trend of ∆WUE\(_i\) with the slope of 0.10 g C kPa per kg H\(_2\)O) in mesic temperate and boreal forests of the Northern Hemisphere, which they attributed to rising atmospheric CO\(_2\) that led to increases in photosynthesis and decreasing ET. However, the observed decline in ∆WUE\(_i\) in our study was more closely related to the increasing trend in AET than any changes in GPP (Fig. 7). Our results suggest that the driving force behind patterns of WUE\(_i\) in drought-prone mature ponderosa pine in the Pacific Northwest differs from those reported for other, more mesic, forest ecosystems in global syntheses. This highlights the importance of considering not only the influence of climate variability on local and regional scales but also site/stand characteristics (such as LAI) and species physiology when predicting ecosystem responses to global change (Fig. 2; Beer et al., 2009; Yang et al., 2016).

Despite the strong dependence of annual WUE\(_i\) on annual precipitation, we found that precipitation pulses of sufficient magnitude in dry summer months can significantly reduce annual WUE\(_i\) (Figs. 6 and 8). Ponderosa pine reacts quickly and dynamically to water availability and even small changes can cause increases in root conductivity and stomatal conductance (Domec et al., 2004). This adaptation led to the increased levels of T as well as lower WUE\(_i\), and WUE\(_{i,T}\) that were observed in response to the summer precipitation pulses in 2004 (Fig. 8).

Although the seasonality in water availability is the primary driver of annual WUE\(_i\), we did not observe any precipitation legacy, defined as the impact of past precipitation on current ecosystem function, at this site as the temporal imposition of water limitation on annual WUE\(_i\) was relieved by the start of wet seasons (winter and spring). Within a given year, drought tended to influence annual WUE\(_i\) to a longer extent than that of non-drought (up to 5 months vs. up to 2 months, Fig. A.4 in Supplementary materials). The apparent lack of prolonged drought effects could be due to the conservative resource allocation strategy adopted by ponderosa pines in this region, which allocates more reserves toward the development of belowground structures for accessing soil water than other species (Williams et al., 2001). This tactic buffers summer droughts and optimizes water use to account for interannual variability in precipitation, which results in relatively stable levels of GPP (Fig. 6B).

5. Conclusion

We investigated climatic and hydrologic effects on WUE\(_i\) and WUE\(_{i,T}\) across climates and stand ages of the predominant forest types (young and mature ponderosa pines and mature Douglas-fir) in the Pacific Northwest. WUE\(_i\) increased with increasing water deficit in the semi-arid young and mature ponderosa pine sites and increasing atmospheric dryness in the mesic Douglas-fir site due to climate variability between locations. Although changes in WUE\(_i\) were dependent on soil water content in both young and mature pines, the similar values of WUE\(_i\) in young and mature ponderosa pines under non-water limited conditions seems to suggest that WUE\(_i\) can be used as a species-specific trait when water availability is high. However, during drought conditions, the mature pine, with its well-established root system, larger stem capacitance, and higher soil water holding capacity, appeared to be better buffered from the effects of seasonal drought. A lower sensitivity of WUE\(_{i,T}\) confirmed the lesser influence of seasonal drought on the mature pine than on the young pine. These results emphasize that, even among trees of the same species, individuals of different ages can have markedly different trends in WUE\(_i\) and WUE\(_{i,T}\) (particularly under drought conditions) and must be incorporated separately into models. Within the evergreen needle-leaf plant functional type, Douglas-fir and ponderosa pine are different enough that sub-plant functional type classes, such as genera, would be a reasonable classification for land system modeling (Law, 2014). Therefore, it is of great importance to
take into account both species- and age-specific values of WUE, and WUE,\(_T\) when developing vegetation models for use in predicting forest responses to drought. In addition to ecophysiological influences on WUE, understanding the role of \(T\) in ecosystem water loss is crucial for the construction of accurate vegetation models. WUE can largely be determined by soil physical processes and ET from understory (e.g., 26% of total ET in spring and 20% in summer at mature ponderosa pine) during drought in open forest canopies but the response of the trees can be masked. For a more precise representation of tree drought sensitivity, a transpiration-specific WUE should be utilized in global change modeling.

In the PNW, the effects of drought and forest developmental stage interact to alter carbon and water exchange across the landscape. The semi-arid portion of the PNW region is projected to experience warmer winters and relatively drier summers in the future (Dai, 2013; Dalton et al., 2013). Precipitation is predicted to change by about 10% in the region from 2030 to 2059 (Mote and Salathé, 2010), which could exacerbate drought conditions in already drought-prone areas. The PNW region experienced severe drought in 2015 and the frequency of these types of events are projected to increase in the near future (Wise, 2016). We are just beginning to have a long enough data record to understand ecosystem responses to drought in the major PNW forest types. Identifying drivers of WUE variability in seasonally water-limited ecosystems encompassing different drought severities over the long-term may help to predict the responses of carbon and water dynamics to climate change in biomes likely to experience similar conditions in the future.

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Appendix A. Supplementary data

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