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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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ABSTRACT

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 (WUE_i) 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 H_2O, respectively). In contrast, annually averaged WUE_i was similar among the sites (2.8 g C kPa per kg H_2O for pines and 2.4 g C kPa per kg H_2O for Douglas-fir). The effect of drought stress on WUE_i was most pronounced in young pine, followed by mature pine and Douglas-fir (32, 11, and 6% increase in WUE_i 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 WUE_i 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 (WUE_{i_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 WUE_i 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

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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 (WUE_i = 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 WUE_i. Although few sites were in dry regions, they observed an increase in WUE_i with short-duration moderate drought. Keenan et al. (2013) also showed a substantial upward trend in WUE_i 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 CO_2 fertilization effect. Most of the global syntheses focus on the changes of WUE_i associated with different PFTs, but few examined WUE_i 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 WUE_i 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_i was ~70% larger in young pine (4 g C kPa per kg H_2O) than mature pine (2.6 g C kPa per kg H_2O) 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 WUE_i, both of which are derived from measurements of ET, at ponderosa pines in semi-arid sites. However, one of the limitations of WUE_i, 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 Kelliher, 1989). Throughout periods of drought, particularly in low LAI forests, WUE_{i_T} (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_i and WUE_{i_T} 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 WUE_i as a plant trait for improving models.

2. Materials and methods

2.1. Study sites

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://ameriflux.ornl.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 (MP), and mature Douglas fir (DF) locations. Numbers in parenthesis indicate the measurement year.

Site	MP	YP	DF
Latitude (°N)	44.451	44.315	44.6465
Longitude (°W)	121.558	121.6078	123.5515
Elevation (m)	1255	1008	263
Mean age (years)	67 (2012)	18 (2004)	41 (2005)
Mean height (m)	17 (2011)	3.1 (2003)	25 (2005)
Density (trees ha^{-1})	325 (2006)	260 (2003)	414 (2006)
Diameter at breast height (cm)	32.3 (2011)	8.3 (2007)	32.1 (2006)
Biomass (g C m^{-2})			
Wood	6293 (2011)	205 (2003)	10036 (2009)
Foliage	535 (2011)	62 (2003)	833 (2009)
Maximum leaf area index	2.8 (2007)	1.8 (2008)	9.4 (2006)
Rooting depth (m)	1.5	0.5	1.0
Foliar C:N	57:1 (2001)	–	36:1 (2003)
Soil $C:N^+$	24:1[a] (2001)	–	22:1[a] (2005)
Soil depth (m)	1.5	0.5	1.0
Soil sand/silt/clay fraction (%)	sandy	loamy sand	silty clay loam
	0.0–0.2 m: 69/24/7	0.0–0.1 m: 80/17/3	0.0–0.2 m: 33/35/32
	0.2–0.5 m: 66/27/7	0.1–0.2 m: 80/17/3	0.2–0.5 m: 29/33/38
	0.5–1.0 m: 54/35/11	0.2–0.5 m: 80/17/3	0.5–1.0 m: 33/35/32
30-year mean[b] annual temperature (°C)	7.5	7.6	10.6
30-year mean[b] annual precipitation (mm)	536	500	1821

[a] Soil C:N ratio at MP and DF was averaged from the measurements at 0–20, 20–50, and 50–100 cm depths.
[b] The 30-year mean (1981–2010) was obtained from the PRISM Group at Oregon State University (http://prismmap.nacse.org/nn/).

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