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To cite this article: Yueyang Jiang *et al* 2019 *Environ. Res. Lett.* **14** 074029

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Environmental Research Letters



LETTER

OPEN ACCESS

RECEIVED

28 November 2018

REVISED

30 May 2019

ACCEPTED FOR PUBLICATION

31 May 2019

PUBLISHED

16 July 2019

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Trends and controls on water-use efficiency of an old-growth coniferous forest in the Pacific Northwest

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Keywords: water-use efficiency, carbon and water fluxes, old-growth coniferous forest, drought, climatic change

Supplementary material for this article is available [online](#)

Abstract

At the ecosystem scale, water-use efficiency (WUE) is defined broadly as the ratio of carbon assimilated to water evaporated by an ecosystem. WUE is an important aspect of carbon and water cycling and has been used to assess forest ecosystem responses to climate change and rising atmospheric CO₂ concentrations. This study investigates the influence of meteorological and radiation variables on forest WUE by analyzing an 18 year (1998–2015) half-hourly time series of carbon and water fluxes measured with the eddy covariance technique in an old-growth conifer forest in the Pacific Northwest, USA. Three different metrics of WUE exhibit an overall increase over the period 1998–2007 mainly due to an increase in gross primary productivity (GPP) and a decrease in evapotranspiration (ET). However, the WUE metrics did not exhibit an increase across the period from 2008 to 2015 due to a greater reduction in GPP relative to ET. The strength of associations among particular meteorological variables and WUE varied with the scale of temporal aggregation used. In general, vapor pressure deficit and air temperature appear to control WUE at half-hourly and daily time scales, whereas atmospheric CO₂ concentration was identified as the most important factor controlling monthly WUE. Carbon and water fluxes and the consequent WUE showed a weak correlation to the Standard Precipitation Index, while carbon fluxes were strongly dependent on the combined effect of multiple climate factors. The inferred patterns and controls on forest WUE highlighted have implications for improved understanding and prediction of possible adaptive adjustments of forest physiology in response to climate change and rising atmospheric CO₂ concentrations.

Introduction

Forest carbon dynamics and water cycling are tightly coupled as plants balance carbon gain against water loss through the regulation of stomatal conductance (Baldocchi *et al* 1987, Baldocchi 1997, Whitehead 1998). The rate of carbon gain per unit of water loss, known as water use efficiency (WUE), has been widely recognized as an important physiological link between carbon and water cycling in terrestrial ecosystems, and used to track and predict ecosystem responses to climate change and the increase in atmospheric CO₂ concentration (Zhu *et al* 2011, Battipaglia *et al* 2013,

Voelker *et al* 2016). Therefore, a comprehensive characterization of WUE responses to climate anomalies (i.e. departures from the long-term average) is crucial for predicting plant responses to future climate change (Seibt *et al* 2008).

WUE has been defined in several ways. In forests, WUE is typically determined either by measuring the stable carbon isotope composition of foliage or tree rings, or by using the eddy covariance method to estimate ecosystem-scale carbon and water fluxes (Monson *et al* 2010, Michelot *et al* 2011, Belmecheri *et al* 2014, Scartazza *et al* 2014, Guerrieri *et al* 2016). Carbon analyses yield estimates of intrinsic WUE

(CO₂ assimilation/stomatal conductance), whereas the eddy covariance-based WUE tracks the ratio of the biometeorological fluxes. Tree-ring isotope data show that the ratio of photosynthesis to stomatal conductance greatly increased in the past century among most forest types, likely attributable to the impacts of rising atmospheric CO₂ concentrations on both photosynthesis and stomatal conductance (Peñuelas *et al* 2008, Andreu-Hayles *et al* 2011). At the ecosystem scale, WUE estimated using the eddy covariance method exhibit a similar increasing trend in a number of temperate and boreal forests of the Northern Hemisphere over the past two decades as a result of reduced ecosystem transpiration (Keenan *et al* 2013). The reduction in ecosystem transpiration is hypothesized to have been driven by a decline in stomatal conductance in response to rising atmospheric CO₂ (Keenan *et al* 2013) and by plasticity in plant functional traits over time (Mastrotheodoros *et al* 2017). Keenan *et al* (2013) point out that the observed increase in forest WUE is beyond empirical estimates and most model predictions. Although the trend of increasing WUE appears to be robust across the forest ecosystems that have been studied, Huntzinger *et al* (2017) argue that the CO₂ fertilization effect might be overestimated in most mechanistic models. These apparently contradictory findings impose high uncertainty in the patterns of WUE in response to climate variability (Reichstein *et al* 2002, 2007, Medrano *et al* 2009), and highlight the knowledge gap in understanding the mechanisms regulating WUE across multiple spatial and time scales (Guerrieri *et al* 2016, Knauer *et al* 2017).

Old-growth forests were estimated to encompass 7.9 Mha in western Oregon and Washington prior to logging, of which 13.1%–17.5% remained by the 1980s (Booth 1991). Currently, these forests are threatened by extreme climate anomalies such as drought and heat stress (Law and Waring 2015). At the Wind River site, a 500 year old evergreen coniferous forest, Jiang *et al* (2019) demonstrate that changes in ecosystem carbon and water fluxes are primarily controlled by tree physiology: high vapor pressure deficit causes stomata to close, thereby lowering transpiration and photosynthesis, which in turn changes WUE over time. In the summer, transpiration at the Wind River site comprises roughly 85% of total water loss (defined here as evapotranspiration which does not include runoff) (Rastogi 2018). Under future scenarios with hotter summers and drier winters (Mote and Salathé 2010, Mote *et al* 2014), less available water during the growing season may alter the balance between transpiration and photosynthesis, thereby altering WUE. Additionally, rising atmospheric CO₂ concentrations may partially offset drying of the climate, as higher CO₂ concentrations reduce evapotranspiration by decreasing canopy conductance (Yang *et al* 2019). Although many possible drivers of WUE have been

identified, the general mechanisms of change remain poorly understood.

This study aims to better understand how WUE of the old-growth forest responds to climate anomalies and long-term shifts in climate in the Pacific Northwest, USA. Given the strong physiological control of climate on carbon and water exchanges at this site (Jiang *et al* 2019), we hypothesize that climate anomalies—in addition to rising atmospheric CO₂ concentrations—drive changes in WUE, and that patterns of meteorological controls vary across different time scales. For example, under increasing atmospheric CO₂ concentration (observed to be +3 ppm yr⁻¹, R² = 0.82), along with possible changes in VPD, we hypothesize that WUE would exhibit a significant increase for the period of 1998–2015. To test these hypotheses, we identify possible trends in WUE and examine the influence of meteorological variables on WUE by analyzing an 18 year (1998–2015) time series of carbon and water fluxes measured with the eddy covariance method.

Data and methods

Study area

Our study area is an old-growth evergreen coniferous forest stand in the Wind River Experimental Forest, located in the T. T. Munger Research Natural Area in the southern Cascade Range of Washington State, USA (45°49'13.76" N; 121°57'06.88" W; 371 m asl). The forest is 450–500 years old and dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) trees (Shaw *et al* 2004). Douglas-fir trees dominate the basal area and upper canopy given their exceptional size and stature—the tallest trees are 67 m in height—while western hemlock trees dominate the stem density of the stand and leaf biomass in the mid-canopy and lower canopy (Shaw *et al* 2004). Within this forest is an 87 m free-standing tower that has been equipped with micro-meteorological and eddy covariance instrumentation that has been in operation since 1998.

At the site, leaf biomass is unevenly distributed in the vertical direction reflecting the complex structure of the old-growth stand (Thomas and Winner 2000, Parker *et al* 2004). Water table depth is seasonally variable and ranges from 0.3 to 0.5 m in the wet winter months to a depth of 2.0–2.4 m in the summer and early autumn (Warren *et al* 2005). Winters are relatively mild and wet, with a mean temperature of 1.8 °C and mean precipitation of 990 mm; whereas summers are dry and warm, with a mean precipitation of 76 mm and mean temperature of 17.7 °C. Due to the strong seasonality of precipitation, total annual precipitation is best described in terms of the water-year, beginning with October and ending in September. Mean annual air temperature is 9.2 °C, and mean water-year precipitation is 2173 mm. Precipitation was measured

daily by rain and snow gauges at the Carson Fish Hatchery near the site (-121.973° , 45.8677°). The measured major climate variables in the growing season (March–September) shows great annual variabilities across the period of 1998–2015 (figure S1 is available online at stacks.iop.org/ERL/14/074029/mmedia).

Data preparation

We obtained half-hourly carbon and water vapor fluxes from gap-filled eddy-covariance measurements taken at the site for the period of 1998–2015 (<http://ameriflux.lbl.gov/sites/siteinfo/US-Wrc>, Wharton 1998–2016). Evapotranspiration (ET) ($\text{g m}^{-2} \text{s}^{-1}$) was calculated from canopy latent heat flux measurements (LE). We suspected that LE may have been underestimated in 2010–2013 measurements due to a calibration error with the infrared gas analyzer (IRGA) (Wharton, personal communication). Therefore, ET was corrected for that period using estimated H_2O concentrations from a humidity sensor (supplemental material SM1). All rainy days and two subsequent days were excluded from the analysis to exclude evaporation from wet leaves and soil surfaces (Grelle *et al* 1997). Thus, we assumed that growing season water flux primarily represented transpiration (Rastogi 2018). Following Wharton and Falk (2016), our analysis focused on daytime periods (8 am–4 pm) from March to September, which avoided measurement technique uncertainties caused by non-ideal atmospheric conditions (e.g. calm, poorly mixed nighttime stable air in the canopy, periods of heavy rain, and ice and snow). We ignored the evaporation of dew since there was no direct way of estimating dew quantity in the absence of leaf wetness measurements throughout the canopy profile. However, H_2O vapor profile measurements from a recent study at the site demonstrate that dew is not a substantial part of the measured ET fluxes in this forest, particularly during the daytime (Rastogi *et al* 2018a).

Methods

To evaluate WUE trends, we defined and compared three metrics of ecosystem-scale WUE. The first metric, photosynthetic WUE (pWUE), was defined as the ratio of gross primary production (GPP) to evapotranspiration (ET). The second metric was inherent water-use efficiency (ihWUE), the ratio of the product of GPP and vapor pressure deficit (VPD) to ET (Beer *et al* 2009). Both pWUE and ihWUE have been widely used to investigate ecosystem-scale responses to environmental change (Law *et al* 2002, Keenan *et al* 2013, Knauer *et al* 2017, Mastrotheodosos *et al* 2017, Wang *et al* 2018). The third metric was the ratio of net ecosystem exchange (NEE) to ET (eWUE), which avoids potential errors in estimating GPP arising from NEE partitioning. For more information on NEE partitioning and the assumptions used to

calculate ecosystem respiration (RE) and GPP at Wind River see Falk *et al* (2008).

We calculated each WUE metric during the growing season at four time scales: half-hourly, daily, monthly, and seasonally. We also examined the inter-annual trend of growing season WUE from 1998 to 2015 for each metric. Due to the strong seasonality of carbon fluxes (Wharton *et al* 2012), we performed the analysis for two periods: (1) March–June, when water is usually not a significant limiting resource; and (2) July–September, when there are stronger atmospheric demands on water availability and soil water may become limiting. Because of possible errors with the IRGA in 2010–2013, we examined trends both before 2010 and for the entire time series, using error-corrected data. To evaluate the effect of incident radiation on WUE, we calculated the ratio of daytime diffuse radiation to total shortwave radiation ($r = R_{\text{diff}}/R_{\text{short}}$), and then categorized days as sunny ($r < = 0.2$), partly cloudy ($0.2 < r < 0.6$), and cloudy ($r > = 0.6$). We used linear regression of WUE on the diffuse ratio r to evaluate the effects of cloudiness.

To estimate the effect of atmospheric conditions on stomatal regulation of ecosystem water fluxes, we calculated canopy conductance (G_c , m s^{-1}) using the inverted Penman–Monteith equation (Monteith 1964, Stewart 1988).

$$G_c = \left[\frac{\rho c_p \text{VPD}}{\gamma \text{LE}} + \frac{\left(\frac{\Delta}{\gamma}\right)\beta - 1}{G_a} \right]^{-1}, \quad (1)$$

where ρ is air density (kg m^{-3}), c_p is specific heat ($\text{J kg}^{-1} \text{K}^{-1}$), VPD is vapor pressure deficit (kPa), γ is the psychrometric constant (kPa K^{-1}), LE is latent heat flux (W m^{-2}), Δ is slope of the saturation vapor pressure curve (kPa K^{-1}), β is the Bowen ratio, and G_a is aerodynamic conductance for momentum transfer ($G_a = u_*^2/U$) (m s^{-1}). All variables were derived from micrometeorological and eddy-covariance data at the half-hourly time scale.

To provide a comprehensive analysis of the relationships among different climate variables and WUE, we used multiple linear regression (MLR) and a machine learning technique called boosted regression trees (BRT) (Elith *et al* 2008) to rank the relative importance of possible meteorological predictors of WUE. The six meteorological variables we examined were VPD, air temperature, soil water content, CO_2 concentration, solar radiation, and wind speed. BRT and MLR were performed at half-hourly, daily and monthly time scales. In general, BRT is less sensitive to variable covariance than MLR, and can detect non-linear thresholds (Olden *et al* 2008).

To explore the influence of drought severity on WUE, we compared GPP, NEP (–NEE) and ET among years with contrasting values of the Standardized Precipitation Index (SPI, McKee *et al* 1993). SPI is

Table 1. Levels of drought severity (McKee *et al* 1993).

SPI value	Class
$SPI \geq 2.0$	Extremely wet
$1.5 \leq SPI < 2.0$	Severely wet
$1.0 \leq SPI < 1.5$	Moderately wet
$-1.0 < SPI < 1.0$	Normal
$-1.5 < SPI \leq -1.0$	Moderately dry
$-2.0 < SPI \leq -1.5$	Severely dry
$SPI \leq -2.0$	Extremely dry

calculated from long-term monthly precipitation time series and represents precipitation drought. An arbitrary averaging period (i.e. 3, 6, 12, 24, or 48 months) is selected to determine the time scale to reflect the impact of drought on the availability of ecosystem water resources. Positive SPI values indicate above normal precipitation while negative SPI values indicate below normal. Because SPI is normalized, it can represent the severity of both wetness and dryness. SPI ranges from -3 (extremely dry) to $+3$ (extremely wet) and is categorized into seven classes representing drought intensities, with values from -1 to 1 considered to be ‘normal’ (table 1, McKee *et al* 1993). SPI compares the accumulated precipitation during a period of i months with the long-term accumulated precipitation distribution for the same accumulation period. However, it should be noted that SPI does not include water losses due to evapotranspiration or runoff and thus likely overestimates water availability at the site.

We calculated SPI based on the long-term precipitation record from 1919 to 2015 following McKee *et al* (1993) and used 6 month SPI to identify seasonal precipitation anomalies that may reflect anomalies in soil water storage for the period of 1997–2015. We averaged the 6 month SPI values for the wet season (November–April) and the dry season (May–September) to identify interannual patterns of drought for the study period 1997–2015. We explore the effects of drought severity on forest productivity by examining drought relationship to carbon and water flux values for two phases of the growing season (GS): early GS (March–June) and late GS (July–September). Based on SPI, we compared the climate anomalies and carbon and water fluxes of three individual years with distinct seasonal drought intensities relative to 1998–2015 average: 2004 (normal early GS, normal late GS); 2006 (normal early GS, severely dry late GS); and 2015 (moderately dry early GS, severely dry late GS).

Results

All three measures of water use efficiency (WUE) calculated during the full growing season (March–September) exhibited statistically significant increasing interannual trends ($p < 0.05$) from 1998 to 2007, based on linear regressions (figure 1). Specifically,

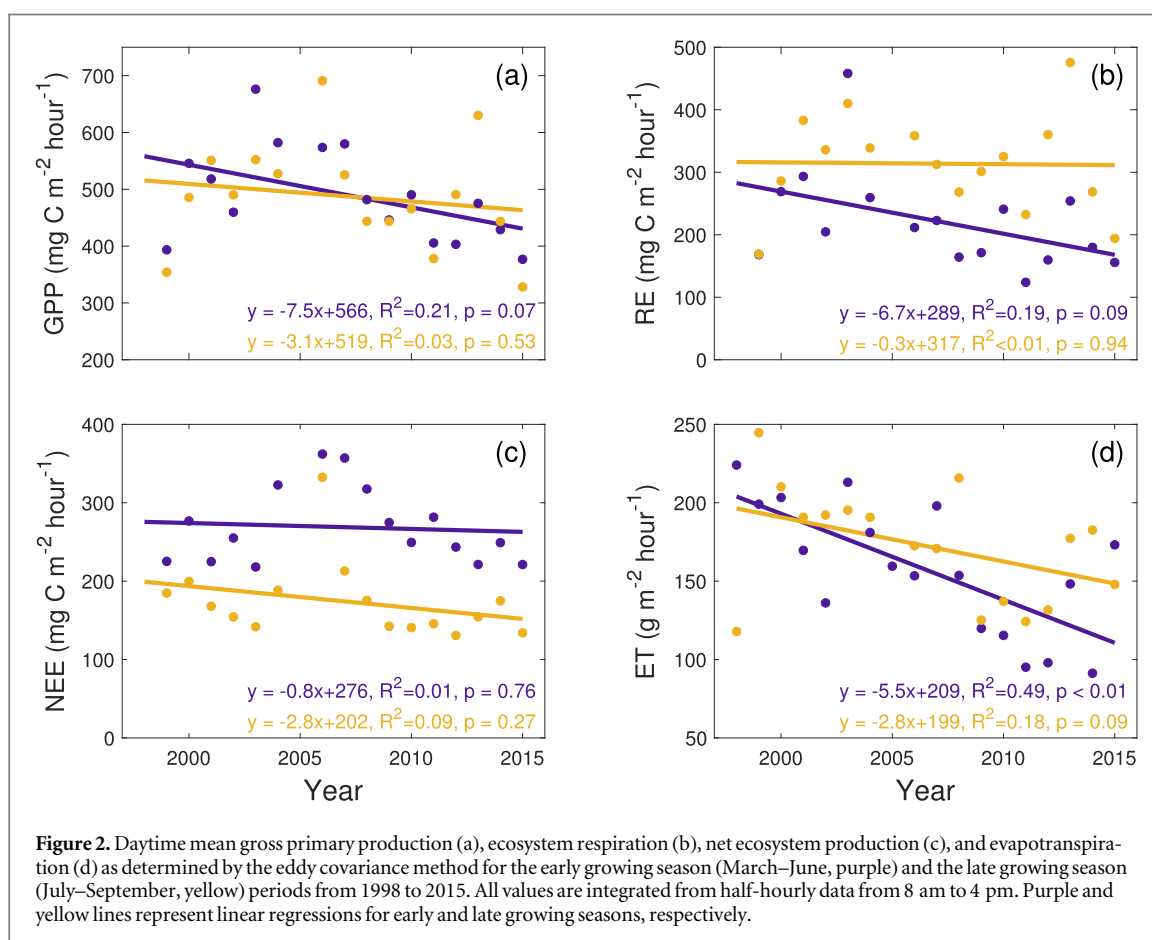
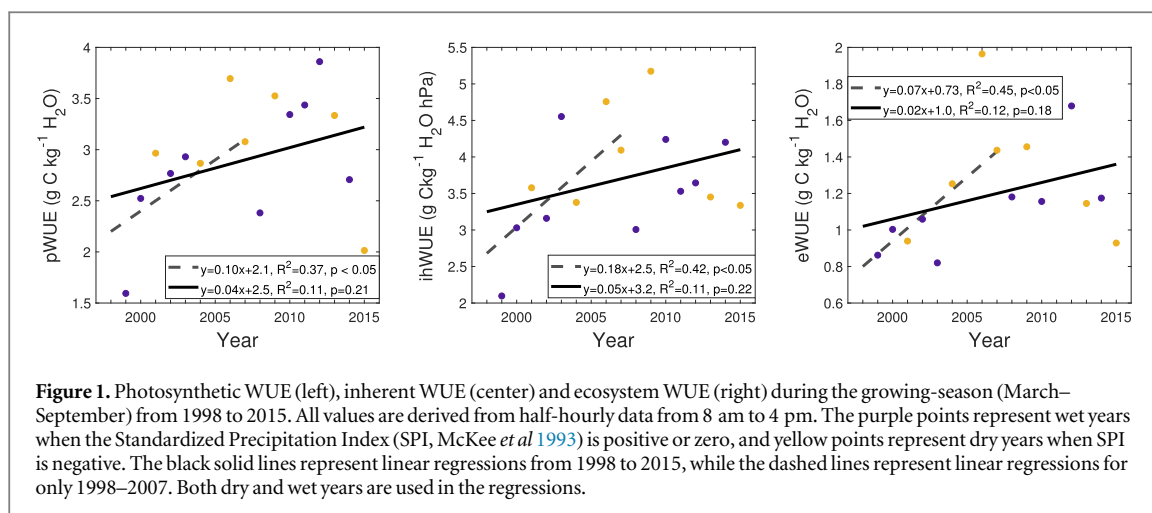
photosynthetic WUE (pWUE) and ecosystem WUE (eWUE) increased 0.1 and $0.07 \text{ g C kg}^{-1} \text{ H}_2\text{O yr}^{-1}$ respectively, and inherent WUE (ihWUE), which directly accounts for VPD, rose by $0.18 \text{ g C kg}^{-1} \text{ H}_2\text{O hPa yr}^{-1}$. However, trends in all three measures of WUE were not statistically significant when the period 2008–2015 was included. In particular, eWUE values appeared to exhibit little trend except for a few high-value years. No WUE metric showed an obvious response to drought severity, as represented by low SPI values, likely because evapotranspiration (ET) is not included in the precipitation index. For example, pWUE and eWUE were exceptionally low in both a wet year (1999) and a dry year (2015).

Examination of individual carbon and water fluxes highlights the drivers of observed interannual patterns of WUE. There were no statistically significant interannual trends in carbon fluxes (GPP, RE, NEP) in either early (March–June) or late (July–September) growing season through the entire 18 year period at the $p = 0.05$ level, although early season GPP declined with a $p = 0.07$ level of significance. Ecosystem water fluxes (ET) in the early growing season decreased significantly ($p < 0.01$) over the 18 year period (figure 2). Larger inter-annual variability of ET also contributed to the lack of significant trends in WUE metrics across the entire record.

Variations in eddy covariance-inferred canopy conductance (G_c) across the record helped clarify ecosystem trends. G_c exhibited a strong trend over the 18 year period, decreasing by 14.4 m h^{-1} or 53% in the late growing season (figure 3(a)). This decline was associated with an overall increasing trend of VPD during the same period ($p = 0.17$, figure 3(b)). Due to large annual variations, G_c and VPD showed no significant trends in the early growing season. Although G_c was estimated by multiple variables changing with time, daily G_c values were tightly correlated with VPD (figure 3(c)). The hyperbolic curves fitted to early and late growing season data were statistically significant and had similar shapes, with G_c being severely constrained above a VPD of 1 kPa.

There was high inter-annual variability in drought severity from 1998 to 2015 (figures 4(a) and (b)). We examined the averaged SPI of the wet season (November–April) to assess accumulated precipitation for the early growing season, and, similarly, the averaged SPI of the dry season (May–September) for the late growing season. For the wet season, there were as many drier-than-normal years as there were wetter-than-normal years. For the dry season, 3 of the 18 years were considered to be drier than normal based on SPI values using the 1919–2015 record (table 1). We found weak ($|\rho| < 0.4$) and statistically insignificant correlations between various ecosystem measures (including the three WUE metrics) and SPI for both early and late growing seasons (figure 4(c)).

Examining periods with contrasting drought severities (as represented by SPI) revealed possible



physiological controls on the timing and magnitude of carbon and water vapor fluxes (table 2). Using the 18 year averaged SPI as a baseline, we selected 2004 as a representative normal year, 2006 as a moderately dry year, and 2015 as a severely dry year. 2004 follows a large carbon source year in 2003 when ecosystem respiration was higher than normal due to higher temperatures but near-normal precipitation. In 2004 SPI values were normal in both the early and late growing seasons. Higher-than-average air temperature (+1.5 °C) and soil water content (SWC, +5.6 m³ m⁻³) led to high GPP (+92 mg C m⁻² h⁻¹)

and NEP (+54 mg C m⁻² h⁻¹) during the early growing season. In the late growing season, VPD was slightly lower than average while SWC and precipitation were higher, and gross productivity and net productivity measures (GPP and NEP) were not significantly different from the 18 year averages.

In 2006, the moderately dry year, SPI values showed 'normal' to 'severely dry' conditions from the early to the late growing season. In that year, although precipitation was considerably lower than the baseline (by -195 mm), higher SWC (+6.2 m³ m⁻³) and greater GPP (+84 mg C m⁻² h⁻¹) and NEP

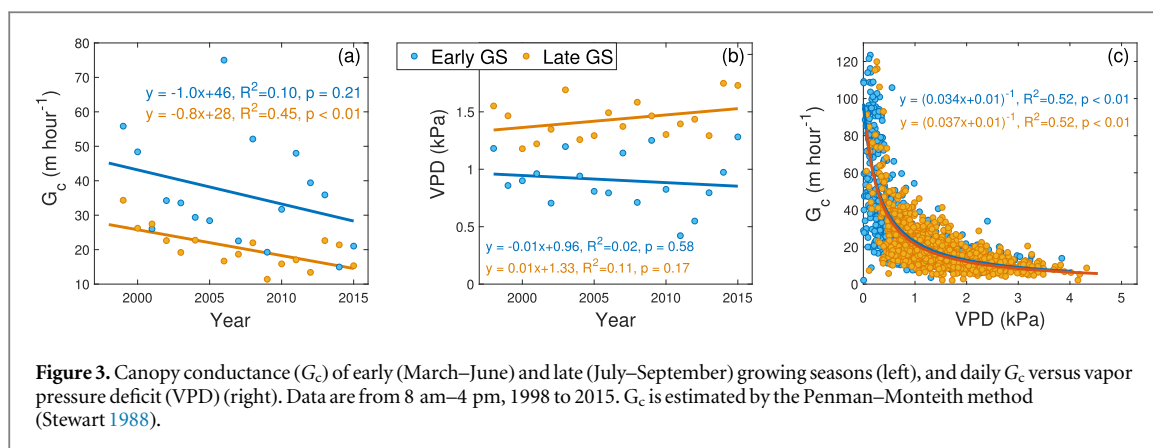


Figure 3. Canopy conductance (G_c) of early (March–June) and late (July–September) growing seasons (left), and daily G_c versus vapor pressure deficit (VPD) (right). Data are from 8 am–4 pm, 1998 to 2015. G_c is estimated by the Penman–Monteith method (Stewart 1988).

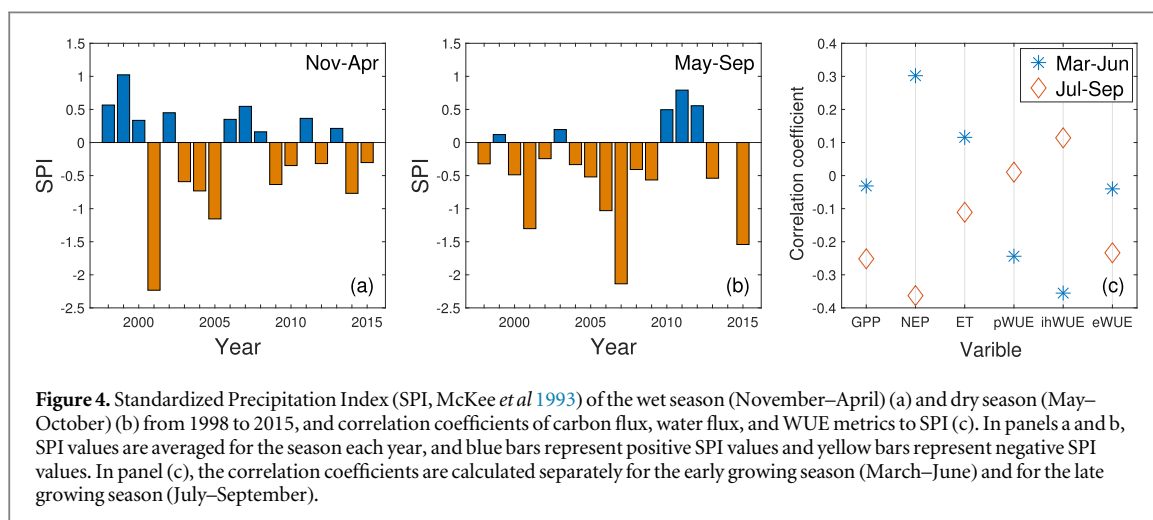


Figure 4. Standardized Precipitation Index (SPI, McKee *et al* 1993) of the wet season (November–April) (a) and dry season (May–October) (b) from 1998 to 2015, and correlation coefficients of carbon flux, water flux, and WUE metrics to SPI (c). In panels a and b, SPI values are averaged for the season each year, and blue bars represent positive SPI values and yellow bars represent negative SPI values. In panel (c), the correlation coefficients are calculated separately for the early growing season (March–June) and for the late growing season (July–September).

($+93 \text{ mg C m}^{-2} \text{ h}^{-1}$) were observed in the early growing season. During the late growing season, although the SPI indicated a severe drought, mild climatic conditions and sufficient SWC led to higher GPP and NEP than normal.

In 2015, a severely dry year, SPI values were ‘moderately dry’ in the early growing season, and ‘severely dry’ in the late growing season. In the early growing season, extremely high air temperatures ($+3.2 \text{ }^\circ\text{C}$) and VPD ($+3.8 \text{ hPa}$) along with very low precipitation (-204 mm) suppressed SWC ($-3.4 \text{ m}^3 \text{ m}^{-3}$), GPP ($-113 \text{ mg C m}^{-2} \text{ h}^{-1}$), and NEP ($-48 \text{ mg C m}^{-2} \text{ h}^{-1}$). In the late growing season, a similar dynamic was observed under a severe drought (SPI = -1.6). Anomalous high VPD ($+3.3 \text{ hPa}$) strongly suppressed GPP ($-159 \text{ mg C m}^{-2} \text{ h}^{-1}$) and NEP ($-40 \text{ mg C m}^{-2} \text{ h}^{-1}$) compared to the baseline. Consequently, the entire growing season in 2015 had substantially lower GPP ($-133 \text{ mg C m}^{-2} \text{ h}^{-1}$) and NEP ($-44 \text{ mg C m}^{-2} \text{ h}^{-1}$) relative to the 18 year average. Evapotranspiration showed no significant differences among the three selected years, implying it is insensitive to precipitation drought at this site.

For each metric of WUE, the strength of associations with environmental variables varied by time scale (e.g. for pWUE, figure 5). Both boosted regression tree (BRT) and MLR identified incoming

shortwave radiation and VPD as the most important variables in regulating the half-hourly pWUE (figures 5(a) and (b)). In the MLR analysis, air temperature was as important as VPD in determining half-hourly pWUE. However, the importance calculated in MLR can be biased by strong variable covariance, therefore it may overpredict the importance of air temperature and VPD, which are highly correlated ($\rho = 0.91$). At the daily scale, BRT and MLR both indicated strong importance of VPD, which was significantly greater than that of any other variable (figures 5(c) and (d)). The importance of canopy conductance (G_c) at the daily and sub-daily time-scale suggested stomatal closure in response to high VPD was the primary mechanism governing pWUE. With both analyses techniques CO_2 concentration emerged as the strongest driver of pWUE at the monthly scale, followed by air temperature (figures 5(e) and (f)). The importance of SWC was much higher at monthly scale than at the daily and sub-daily scale. A possible explanation for the importance of CO_2 was that in certain months of the year (usually in the spring) there was plentiful water and radiation at this site, and therefore CO_2 concentration played a pivotal role in enhancing photosynthesis and thereby pWUE.

Both BRT and MLR analyses indicated that air temperature primarily controlled half-hourly eWUE,

Table 2. Standard precipitation index (SPI), environmental conditions, and ecosystem fluxes for selected years. In year 2004 SPI values are ‘normal’ in both early and late growing seasons (McKee *et al* 1993, table 1). In year 2006 SPI values transition from ‘normal’ to ‘severely dry’ from the early to the late growing season. In year 2015 SPI values are ‘moderately dry’ in the early growing season, and ‘severely dry’ in the late growing season. Values other than SPI are shown as anomalies from 18 year (1998–2015) averages. An anomaly is shown when it is greater than or equal to 1σ of the 18 yearly values; otherwise it is considered insignificant and marked by *. Environmental conditions include air temperature (T_{air}), vapor pressure deficit (VPD), soil water content (SWC), and precipitation (PPT). Ecosystem fluxes are gross primary productivity (GPP), evapotranspiration (ET), and net ecosystem productivity (NEP).

	Early growing season (March–June)			Late growing season (July–September)			Growing season (March–September)		
	2004	2006	2015	2004	2006	2015	2004	2006	2015
SPI	−0.8	0.3	−1.1	0	−1.8	−1.6	−0.5	−0.6	−1.3
ΔT_{air} (°C)	1.5	*	3.2	*	*	0.8	*	*	2.1
ΔVPD (hPa)	*	*	3.8	−2.9	*	3.3	*	*	3.5
ΔSWC ($m^3 m^{-3}$)	5.6	6.2	−3.4	10.0	*	−4.4	7.7	4.4	−3.6
ΔPPT (mm)	*	−195	−204	191	*	*	*	−262	−245
ΔGPP ($mg C m^{-2} h^{-1}$)	92	84	−113	*	204	−159	*	135	−133
ΔET ($g m^{-2} h^{-1}$)	*	*	*	*	*	*	*	*	*
ΔNEP ($mg C m^{-2} h^{-1}$)	54	93	−48	*	159	−40	*	121	−44

likely due to its strong control on ecosystem respiration (figure S2). MLR also identified VPD having a similar importance as air temperature, owing to the dependence of VPD on air temperature, and because MLR cannot decompose their correlation. At daily and monthly scales, CO_2 concentration had the greatest importance on eWUE in the BRT analysis. In contrast, the MLR analysis showed that air temperature and VPD strongly controlled daily eWUE, while CO_2 concentration was most important at the monthly scale. The same analysis for ihWUE showed that air temperature had an overwhelming effect on ihWUE at half-hourly and daily time-scales (figure S3). This was probably due to the high correlation between air temperature and VPD, which is a variable in the calculation of ihWUE. At the monthly time scale, BRT indicated that CO_2 concentration and radiation were equally important and largely controlled ihWUE. MLR additionally included air temperature along with CO_2 concentration and radiation as the strongest controls on ihWUE on the monthly time scale.

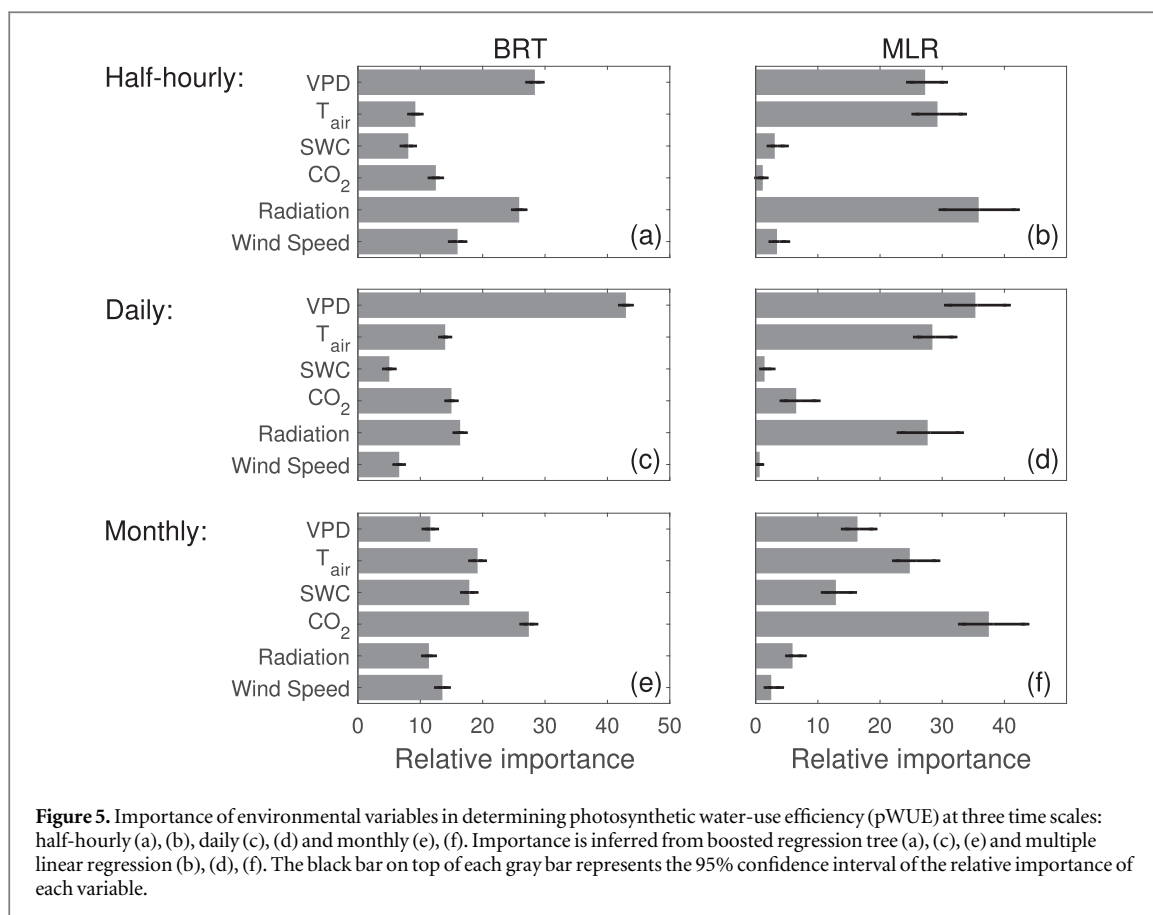
We explored the influence of incident radiation on WUE by linearly regressing daily pWUE and eWUE on cloudiness, as represented by the ratio of diffuse radiation to total shortwave radiation (figure 6). Daily pWUE and eWUE both significantly increased with cloudiness, although with some variability. Average pWUE values within the diffuse ratio bins representing sunny, partly cloudy, and cloudy days were 1.7, 2.6, and 3.7 $g C kg^{-1} H_2O$, respectively, and eWUE averages were 0.6, 1.6, and 2.7 $g C kg^{-1} H_2O$, respectively. A 10% proportional increase in the diffuse light metric (R_{diff}/R_{short}), i.e. a change in the diffuse ratio of 0.1, corresponded to a $\sim 0.3 g C kg^{-1} H_2O$ increase in pWUE and eWUE. A similar analysis determined that ecosystem respiration was only weakly related to the diffuse light metric.

Discussion

All three metrics of ecosystem-scale WUE increased between 1998 and 2015, with significant increases restricted to the period before 2008. Between 2008 and 2015 a proportionally greater reduction in GPP relative to ET slowed the rate of increase in WUE and thus statistically significant WUE trends across the entire record disappeared. In this section, we focus on discussing the mechanisms that influence GPP and ET and control variation in WUE, including forest responses to drought.

What mechanism drives WUE across different time scales?

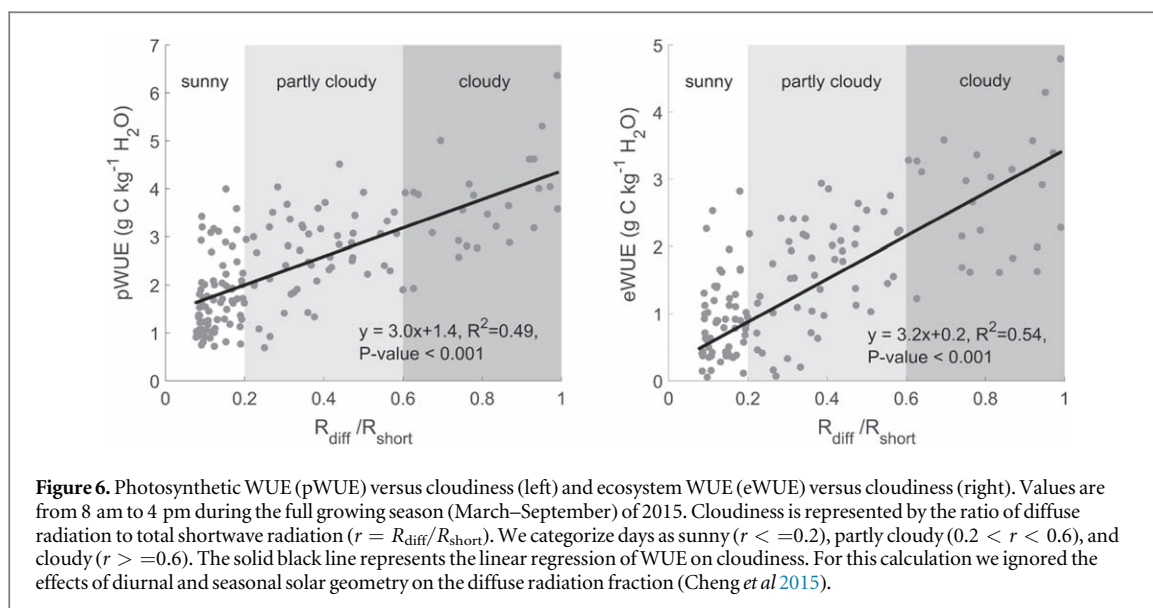
WUE metrics showed a time-scale dependence on the external environment. In general, VPD and air temperature controlled all three WUE metrics at half-hourly and daily time scales, while atmospheric CO_2 concentration was identified as the most important indicator of monthly WUEs. Our analysis of variable importance using a machine learning technique (BRT) and a traditional statistical method (MLR) partly agree with a wavelet cross-correlation analysis by Wagle *et al* (2016), which indicates that variations in carbon uptake and evapotranspiration mostly resonate with VPD and air temperature from half-hourly to weekly timescales. The high dependence of WUE on VPD at sub-daily and daily time-scale implies a strong impact of atmospheric water demand on stomatal conductance which directly affects transpiration and indirectly affects photosynthesis. This hydraulic constraint can be evidenced by the diurnal measurements of stomatal conductance from the Wind River crane, which showed that it peaks relatively early in the day at about 8:30 am and then declines fairly sharply to an afternoon plateau (Woodruff *et al* 2007, Domec *et al* 2008). A linear regression indicates that the day-time



mean VPD has significant negative relationships with pWUE and eWUE at our site. At the daily timescale, the positive correlation of diffuse fraction (driven principally by variations in cloudiness) and pWUE is likely a function of direct and indirect controls (Knobl and Baldocchi 2008, Still *et al* 2009). Increased cloud cover lowers ET by reducing VPD and net radiation. Furthermore, there is less self-shading within the canopy on cloudy days because of the higher proportion of diffuse or reflected radiation. Therefore, needles lower in the canopy may actually have access to higher photoactive radiation (PAR) than on cloud-free days, even though total radiation at the top is decreased, as the needle-leaf canopy is highly efficient in utilizing diffuse and direct radiation for photosynthesis. In other words, higher light use efficiency occurs in lower incident PAR days (Wharton *et al* 2009). Consequently, although photosynthetic rates are lower at the canopy top, the rates increase at lower levels of the canopy due to less shading, thereby increasing overall canopy photosynthesis on cloudy days (Rastogi *et al* 2018b). This is particularly true for forests like Wind River where leaf area is high and distributed in a complex manner along the vertical axis (Parker *et al* 2004).

When integrated to the monthly scale, the importance of VPD control is reduced and partly replaced by the importance of CO₂ concentration and air temperature as controls. At our study site, CO₂ concentration can fluctuate by 40–60 ppm between spring and

summer. Relative to the growing-season mean of ~380 ppm, this 10%–15% seasonal variation can substantially affect photosynthesis, which responds to CO₂ non-linearly. Annually, water supply and demand, and radiation conditions are relatively stable, whereas photosynthetic potential is still not carbon-saturated. Under such conditions, CO₂ concentration can have a strong positive correlation with all three WUE metrics over longer time scales. While it remains unclear to what extent this forest is CO₂ limited, our results indicate that the long-term influence of CO₂ fertilization in this ecosystem requires further investigation. Furthermore, while the period of observation in this study is relatively short, our observations of decadal-scale changes in WUE are in agreement with Keenan *et al* (2013), that the strongly declining G_c suggests a substantial CO₂ impact, along with increasing VPD. The relatively stable water content in deep soil layers (Warren *et al* 2005), time lags between precipitation and water storage, and the ability of large trees to extract deep soil water with deep roots, likely limited the influence of SWC on monthly WUE. Although soil moisture has been widely shown to be correlated with pWUE on an annual basis (Beer *et al* 2009, Yang *et al* 2013), our results suggest that atmospheric CO₂ concentration is the most important indicator to predict long-term trends in pWUE, as well as the other two WUE metrics at this site. Furthermore, air temperature and VPD are highly correlated during the growing season and temperatures are the primary driver of



inter-annual variation in tree-ring carbon isotope discrimination for other forests of the Pacific Northwest (PNW) (Ratcliff *et al* 2018). Therefore, a combination of air temperature (and thus VPD) and CO_2 concentration can capture a large proportion of the variations in WUE at long time scales (e.g. decades or centuries), at least for PNW old-growth forests.

How does an old-growth coniferous forest respond to drought?

Despite the Pacific Northwest being known for abundant winter and spring precipitation, droughts can span cool and warm seasons and thereby impose major physiological stress on trees across the region (Franklin and Waring 1980). The combination of high VPD and air temperature appears to be a major factor that limits GPP and thus reduces ecosystem-scale WUE. Although increased sensitivity to a shortfall in spring precipitation has been recorded elsewhere by tree growth responses to drought timing (D'orangeville *et al* 2018), our study did not find a high correlation between spring SPI with carbon and water fluxes, likely due to the time lags in precipitation and soil water content. The insensitivity of ET to drought severity (as represented by SPI) is likely due to the ability of the mature trees to access water in deep soil layers. As indicated by Warren *et al* (2005), roots at depths greater than 60 cm accounted for 50%–80% of water uptake under drying conditions especially during the driest part of the growing season. Therefore, plant transpiration remains relatively stable in summer because large trees can extract water from progressively deeper soil layers (e.g. down to at least 2 m) where soil water content remains fairly constant (Domec *et al* 2004, Meinzer *et al* 2007). Our data indicate that when air temperatures are anomalously high during a dry summer, as in 2015, decreased GPP is further exacerbated by stomatal closure in response

to higher VPD and also likely by downregulation of enzymes (Wohlfahrt *et al* 2018), resulting in substantially lower pWUE. This finding agrees with the wavelet analysis by Wagle *et al* (2016), which indicates that carbon uptake (NEP or GPP) is constrained more than ET by VPD through restriction of stomatal regulation. This finding also echoes Reichstein *et al* (2002, 2007), which documents a decrease in WUE at European evergreen needleleaf forests during drier years. Meanwhile, high temperatures decrease net carbon uptake and therefore eWUE, due to an increase in ecosystem respiration (Valentini *et al* 1995, Atkin *et al* 2007, Guerrieri *et al* 2016).

Climate projections for the PNW (Mote and Salathé, 2010, Mote *et al* 2014), predict a hotter and drier climate, with less water coming from the winter snowpack (Mote, 2006) and earlier spring snowmelt (Stewart *et al* 2005, Abatzoglou *et al* 2014). Moreover, closed canopy forests of this region tend to have lower snowpack (Dickerson-Lange *et al* 2017). Therefore, it is expected that summer water stress may have a large impact on carbon fluxes of PNW forests in the future. Currently, relatively stable moisture in deep soil layers supports the water demands of tall trees at Wind River during the largely rain-free summer months. However, maintenance of the deep soil water storage may be reduced during a long-term drying climate. Prolonged and severe drought events could eventually result in tree mortality (Mueller *et al* 2005, Anderegg *et al* 2013, 2014), with a particular risk of xylem hydraulic failure in old trees (Adams *et al* 2017). Although drought has not caused substantial tree mortality at our study site, the on-going drying trend may slow the expected transition to dominance by western hemlock, which prefers wetter environments than Douglas-fir. That in turn may feedback to ecosystem-scale WUE.

Conclusion

Ecosystem-scale water-use efficiency (WUE) estimates derived from eddy covariance flux measurements displayed an overall increase between 1998 and 2015 at an old-growth coniferous forest site in the PNW. However, between 2008 and 2015 a proportionally greater reduction in GPP relative to ET slowed the rate of increase in WUE compared to the earlier portion of the record. The strength of associations among individual meteorological variables and WUE varied according to the scale of temporal aggregation. In general, VPD and air temperature control WUE at half-hourly and daily time scales, while atmospheric CO₂ concentration is identified as the most important indicator of monthly WUE. All metrics of WUE show a weak correlation to SPI, while carbon fluxes depend strongly on the combined effect of different climatic factors. The observed patterns and controls on forest WUE have implications for predicting adaptive adjustment of forest physiology in response to climate change and rising atmospheric CO₂ concentrations. Further efforts are needed to monitor the effect of microclimate on WUE across different canopy layers to separate responses of different species to climate anomalies, such as drought.

Acknowledgments

We thank Dr Ken Bible of the Wind River Canopy Crane Research Facility for facilitating this study. Yueyang Jiang is supported by a joint-venture agreement (14-JV-11261952-100) between Oregon State University (OSU) and the USDA Forest Service Pacific Northwest Research Station. John B Kim is supported in part by USDA Forest Service Western Wildland Environmental Threat Assessment Center (WWETAC). Lawrence Livermore National Laboratory is operated by Lawrence Livermore National Security, LLC, for the US Department of Energy, National Nuclear Security Administration under Contract DE-AC52-07NA27344.

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