

## RESEARCH ARTICLE

# Measurement and prediction of water consumption by Douglas-fir, Northern California, USA

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**Abstract**

Douglas-fir (*Pseudotsuga menziesii*) is an important component of mixed-conifer forests of the Western United States. Changes in forest composition from Douglas-fir encroachment in areas of fire-suppression could have implications for water balance, supply and stream habitats. Increasing episodes of severe drought linked to climate change threaten forest health. Measurements of tree water inform management and biosphere models. Twenty-six trees were instrumented with thermal dissipation sapflow probes. Sites were in Petrolia, California, and Maple Creek, California. Monitoring took place from Summer 2015 through Summer 2016. Daily water use was found to decline steeply over each summer dry period. This may limit the influence of Douglas-fir on soil moisture budgets and streamflow during this time period. Tree size, peak and low flow daily water use averages were statistically related. Little difference was found between drier 2015 and wetter 2016 years. However, larger trees showed greater peak water use in 2015, perhaps from sufficient moisture and greater insolation, and at Petrolia, larger trees showed greater dry period water use in 2016, as greater moisture levels persisted into the summer. Linear mixed effects models of daily integral sap velocity (cm/day) were created with the input variables of solar radiation, vapour pressure deficit (VPD) and soil moisture. The best model using Akaike information criterion scores had fixed effects of solar radiation and VPD. This model was trained on one site and then validated at the second site with goodness of fit tests. The model is provided for estimating Douglas-fir water use.

**KEYWORDS**

Douglas-fir, forest management, linear mixed effect models, *Pseudotsuga menziesii*, sapflow, thermal dissipation probe, transpiration, water use

## 1 | INTRODUCTION

Detailed understanding of forest water use grows increasingly important in the face of climate change. California experienced considerable tree mortality during the drought of 2012–2015. As drought progressed, more and more regions of California experienced conditions severe enough to affect tree survival (Asner et al., 2016). Many regions of the world have experienced drought-related tree mortality (Allen et al., 2010).

Additionally, summer stream flow has been declining in recent decades in Northern coastal California (Asarian & Walker, 2016)

across the Pacific Northwest (Luce & Holden, 2009; Sawaske & Freyberg, 2014) and in other parts of the world (Martínez-Fernández et al., 2013). The decline affects endangered aquatic species and the availability of water for agriculture (Deitch & Dolman, 2017), and this decline may be tied to changing forest water use in addition to changing climates.

The climate change link to declining flows is the most obvious, as hotter and drier summers promote greater evapotranspiration losses (Sawaske & Freyberg, 2014) and seasonal changes in precipitation reduce water inputs (Asarian & Walker, 2016). Indeed, Pascolini-Campbell et al. (2021) report that from 2003 to 2019,

evapotranspiration increased globally by 10%. Extension of the growing season may play a factor in increased water use by forests (Hwang et al., 2018).

However, the decline has also been observed to be occurring independently of changes in rainfall and in regions without significant water diversions for irrigation. Furthermore, pristine areas with minimal alteration of forest composition have less noticeable declines. These observations suggest that factors such as forest composition and density that are influenced by forest management decisions may be driving factors in declining streamflows (Asarian & Walker, 2016).

For example, modelling and sapflow measurements on Douglas-fir (*Pseudotsuga menziesii*) in Northern California (Stubblefield et al., 2012) suggest that younger forests may use more water than older forests because of higher stand densities and greater sapwood area to heartwood area ratios. Moore et al. (2004) found that older Douglas-fir forests in Oregon used less water than younger forest because the older forests had fewer stems per hectare as a result of disturbance and had less efficient xylem chambers.

Accordingly, it has been suggested that forest thinning could be used to increase forest resilience to drought (Knapp et al., 2021). Knowledge of tree water use with respect to critical soil moisture thresholds and atmospheric conditions is needed to allow researchers to understand and predict patterns of tree mortality under future climate change (Goulden & Bales, 2019; Marchand et al., 2020) and provide inputs and verification for models of regional forest transpiration and water balance including streamflow. These models can be used to inform forest management decisions.

Douglas-fir trees are an important member of the mixed-conifer forests of California and the Western United States. Thus, the first objective of this study is to quantify water use for individual Douglas-fir trees, to provide foundational data in support of forest management decisions with respect to water resources. Variation in water use will be examined with respect to tree size and seasonality.

To support these efforts, the second objective of this study is to develop and evaluate a model of Douglas-fir water use. The aim is to develop and test the model as a tool for researchers or managers seeking to make water use predictions for their region and time period of interest.

In this study, we instrumented 26 Douglas-fir trees with sapflow probes at two sites in coastal Northern California, with different rainfall regimes. Previous work with Douglas-fir in this region includes measurements in the upper Mattole River watershed (Stubblefield et al., 2012) and in the Elk River watershed (Link et al., 2014). Thermal dissipation sapflow probes have been widely implemented for this purpose since their development by Granier (1987). The trees were monitored from the 2015 dry season through the following winter and spring, and into the 2016 dry season. We compare average daily water use for trees of different sizes for the different seasons and between the two sites.

To investigate the role of weather variables as predictors of tree water use, linear mixed effects models were developed of tree water use driven by environmental variables. The most accurate model was

trained using input variables from one site, and then tested with data from the second site.

## 2 | METHODS

Sapflow rates of 26 Douglas-fir trees of varying sizes (with diameter at breast height [DBH] ranging from 17 to 104 cm) were measured at two locations in the summer of 2015 and the spring and summer of 2016 (Figure 1 and Table 1). This study was performed on two sites in Humboldt County, Northern California, USA: the L.W. Schatz Demonstration Tree Farm near Maple Creek in northern Humboldt County and on private land near Petrolia in southwestern Humboldt County. The Schatz site belongs to the Mad River watershed and the coastal site is within the Mattole River watershed. Both sites have stands consisting dominantly of Douglas-fir of varying ages and densities.

The Petrolia site is located at 40°17'08"N 124°18'28"W. The stand sampled is at a northwest aspect (28°) and at 42° slope. The soil type is gravelly loam and belongs to the hydrologic soil type B, which have low runoff potential and a water table below 80 cm depth (United States Geological Survey [USGS], [websoilsurvey.nrcs.usda.gov](http://websoilsurvey.nrcs.usda.gov)).

The Schatz site is located on the Schatz Tree Farm, southeast of Korb, California (40°46'30"N 123°51'58"W). The stand sampled is at a northwest aspect (14°) and a 42° slope. The soil type is gravelly clay loam and is typically xeric in nature during summer drought periods with high runoff potential year-round (USGS).

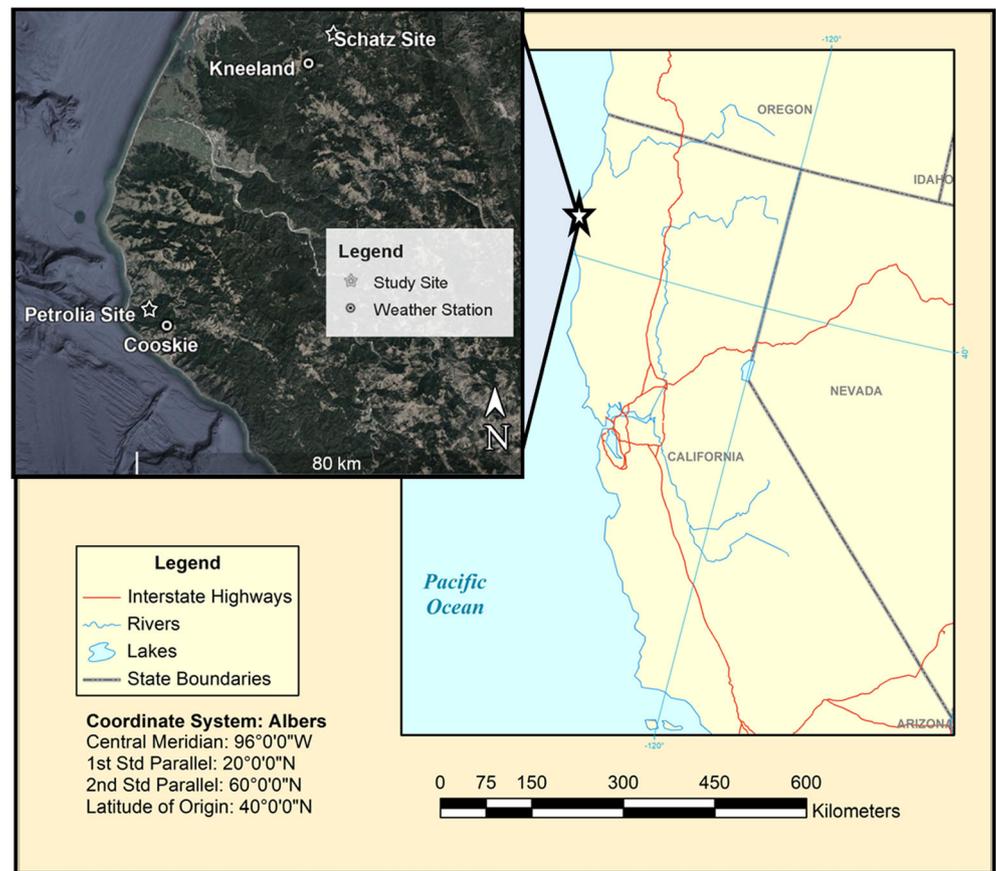
Although both basins have a Mediterranean climate with cool rainy winters and hot dry summers, the Petrolia watershed receives higher annual rainfall and has greater fog influence. In the 2015 water year, 139 cm of precipitation fell in Petrolia, compared to 244 cm over the 2016 water year. The mean precipitation is 190 cm (National Weather Service [NWS]).

At the Schatz site, 119 cm of precipitation fell in 2015, while 162 fell over the 2016 water year. The average rainfall is 137 cm (NWS).

Precipitation, temperature, relative humidity and solar radiation data were obtained from Remote Automatic Weather Stations (RAWS, <https://wrcc.dri.edu/>) located in Kneeland, (40°43'10"N 123°55'42"W) for the Schatz site and Cooskie Mountain, (40°15'25"N 124°15'58"W) for the Petrolia site. Vapour pressure deficit (VPD) was calculated from relative humidity and temperature data using the method described by Allen et al. (1998).

Trees monitored at the Schatz site were part of a larger experiment examining the impact of thinning on tree growth and seedling water balance (Berrill et al., 2018; Kerhoulas et al., 2020). The site received thinning treatments in the fall of 2014. Thinning treatments were implemented at the Petrolia site in 2009. To evaluate competition, local density was calculated (Table 1). At both the dry and wet site, total basal area was determined for neighbouring trees within 6 m of the monitored tree. This distance was deemed to encompass roots from neighbouring Douglas-fir trees competing for the same

**FIGURE 1** Study site locations: Petrolia and Schatz Tree Farm, Northern California, USA



**TABLE 1** Sample tree properties, sapflow sensor length and local density

Petrolia site						Schatz site					
Tree	DBH (cm)	Sapwood thickness (cm)	Sapwood area (cm <sup>2</sup> )	Sensor length (cm)	Local density <sup>a</sup> (cm <sup>2</sup> )	Tree	DBH (cm)	Sapwood thickness (cm)	Sapwood area (cm <sup>2</sup> )	Sensor length (cm)	Local density <sup>a</sup> (cm <sup>2</sup> )
P1	32	3.7	290.6	3	602	S1	46	5	617.6	3	NA
P2	38	7.5	614.8	5	8476	S2	17	3.9	133.8	3	1642
P3	42	6.3	635.5	5	15,834	S3	55	6.5	897.8	5	0
P4	23	2.8	178.5	3	NA	S4	43	3.4	385.9	3	6458
P5	43	3.2	384.4	3	8938	S5	46	8.7	968.1	5	NA
P6	54	6.7	998.8	5	NA	S7	34	4.8	371.5	3	NA
P7	52	4.7	667.8	5	15,608	S9	60	4.4	714.5	3	910
P8	65	5.3	1461.3	5	NA	S10	64	5.1	859.7	3	NA
P9	104	12	3720.6	8	4030	S12	92	7	1747.3	5	NA
P12	79	9.2	1994.3	8	13,860	S33	39	5.1	469	3	10,956
P14	76	10.8	2296.7	8	4838	S35	55	5.8	814.8	5	0
						S38	40	4.7	507.6	3	1051
						S39	37	9.1	705.4	5	NA
						S40	58	4.9	725.9	3	NA
						S43	60	6.7	1038.8	5	7394

<sup>a</sup>Basal area of neighbouring trees within 6 m of sample tree.

water within the soil profile (Mauer & Palátová, 2012) and therefore, an appropriate reflection of local density.

Sapflow measurement using thermal dissipation probes was used to record sapflow velocities and quantify water consumption (Granier, 1987; Lu et al., 2004). At the Schatz site, probes were installed on 25 April 2015 and removed on 13 September 2016. At the Petrolia site, probes were installed on 20 April 2015 and removed on 24 October 2016. The trees were monitored continually during this time period, although occasional power outages or equipment failure (typically damage to probes or cables) resulted in periods of no data recorded for individual trees. Average values were calculated for time periods in late spring/early summer (~June to July) to represent peak water use, late summer/early fall (~August to October) to represent minimum water use and winter/spring (~November to March) to represent wet season water use.

This method has been validated with other techniques (Lu et al., 2004). A pair of linked probes is inserted into holes drilled into xylem tissue. One probe has a heating element and a thermocouple wire, which is cooled in proportion to the amount of sap flowing through the sapwood area, while the second probe measures the ambient sap temperature as a reference. Probes were wired to Campbell Scientific CR1000 data loggers (Logan, UT). Thermal shielding was installed on each tree.

The differences in probe temperatures correspond to sapflow rates (Davis et al., 2012). Average sapflow velocity  $V$  (cm/s) is calculated as follows:

$$V = 0.0119 * K^{1.231} \quad (1)$$

where the dimensionless parameter  $K$  is calculated as follows:

$$K = (\Delta T_m - \Delta T) / \Delta T \quad (2)$$

and  $\Delta T$  is the measured difference in temperature ( $^{\circ}\text{C}$ ) between the heated probe and the reference probe and  $\Delta T_m$  is the maximum value of  $\Delta T$  when sapflow is zero within a 24-h period. Sapflow velocity is converted to sapflow rate ( $\text{cm}^3/\text{s}$ ) by multiplying  $V$  by tree sapwood area.

Temperature readings were taken every 60 s, and the average recorded by data loggers every 30 min throughout each sample period.

It is important to note that the wound created by the insertion of sapflow probes can cause changes to wood physical and thermal properties, resulting in an underestimation of sapflow rates, particularly in ring-porous hardwoods. Wiedemann et al. (2016) found that for oak and beach, sapflow measurements dropped during the 2 weeks subsequent to probe insertion but then reached a steady state with no further decline in accuracy. A wounding correction factor (e.g., Ambrose et al., 2010) was not used in this study.

Sapwood thickness was calculated from increment borer samples. An assumption was made that equal sapflow rates were occurring on different sides of the trunk and thus the use of one tree core and one sensor pair per tree was sufficient. This assumption was held to be

reasonable because inspection of stumps resulting from thinning activities indicated a high degree of symmetry in the radial thickness of the sapflow. DBH was also measured for each tree to obtain tree radius. Bark thickness and heartwood radius were subtracted from the total radius to obtain a sapwood radius that was then used to calculate sapwood area:

$$SA = \pi(Rt^2 - Rh^2) \quad (3)$$

where  $SA$  is sapwood area,  $Rt$  is tree radius (minus bark thickness) and  $Rh$  is heartwood radius. The sapflow rate was then calculated by summation over the sampling period. For comparison, we calculated daily averages for time periods representative of peak flow rates during late spring, minimum flow rates during late summer and the spring rainy period.

Probe lengths of 3, 5 or 8 cm were selected to match sapwood thickness as closely as possible (Table 1). Trees S9, S12 and S14 were fitted with longer probes containing two thermocouples, measuring sap velocities at different radial depths within the sapwood. The data from the two radial depths were averaged for the analysis following the work by Ambrose et al., 2010. Probes were installed with a 1-cm gap to allow for growth during the course of the study.

Soil moisture was determined using biweekly gravimetric sampling (Black, 1965). Samples were taken at three locations at each site from a depth of 15 cm. Splining techniques were used to interpolate daily soil moisture levels from the biweekly data.

We used Matlab (MATLAB and Statistics Toolbox Release, 2016) to perform a linear mixed effects analysis of the relationship between daily water use and solar radiation, soil moisture and VPD (Bolker et al., 2009). These model inputs were chosen on the basis of the findings of a more extensive analysis of forcing variables for sapflow performed by Link et al. (2014), and because the data are readily available for this study, and for the estimation of sapflow for other applications using the model developed here.

As fixed effects, we entered solar radiation, soil moisture, date and VPD (without interaction term) into the model. As random effects, we used intercepts for trees, season (2015 or 2016) and site. Akaike information criterion (AIC) (Akaike, 1973) was used to rank model performance.  $P$  values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question. Hourly sapflow data were integrated to create daily water use values. Other data values were obtained in daily form as that is what is typically available from meteorological networks. For the modelling, the summer dry period (25 April to 13 September) was chosen to eliminate complications from rainfall. Two steps were taken to minimize variations due to tree size or individual differences between trees (Link et al., 2014). The first was modelling sap velocity rather than water use. Sap velocity, the rate at which sap rises in the xylem ( $\text{cm}/\text{day}$ ), is multiplied by sapflow area in order to estimate the volume of water use ( $\text{ml}/\text{day}$ ). The second step was normalization, whereby each daily data point was divided by the 99.5th percentile value recorded for that tree. The 99.5th percentile was chosen instead of

the maximum to avoid outliers. This step removes the variation in water use between trees owing to size from the model.

Model prediction accuracy was tested by running the linear model on input data from the 15 instrumented at the Schatz Tree Farm for 2015 and 2016, and then using the model to predict tree water use for the 11 instrumented trees at the Petrolia site. Model accuracy and fit was tested using goodness of fit parameters: Nash–Sutcliffe efficiency (NSE) test (Nash & Sutcliffe, 1970), RMSE-observations standard deviation ratio (RSR) (Legates & McCabe, 1999), and percent bias (PBIAS) (Gupta et al., 1999) and assessment ranges for these metrics provided in Moriasi et al. (2007).

### 3 | RESULTS

Douglas-fir water use measurements indicate a dramatic drop in transpiration taking place over the course of the seasonal dry period, with maximal rates in early summer declining steadily to minimal water use in August through October. Trends in daily tree water consumption for representative trees from each site are shown in Figure 2. To more clearly distinguish trends, the figure uses a 7-day moving average of integrated daily water use.

Average daily water use (L/day) during periods representative of late spring peak water use and late summer minimal water use were calculated for 2015 and 2016 (Table 2). Continued monitoring during early 2016 allowed for the estimate of average water use during winter/early spring 2016 as well. Average daily water use is presented rather than seasonal totals as some trees had incomplete the data records due to equipment malfunction. Tree DBH is shown. As a measure of the upper bounds of tree water use, the 99.5th percentile daily water use values are presented. The 99.5th percentile sap velocities (cm/day) used for the modelling section are also presented.

The seasonal water use decrease mirrors declines in solar radiation and soil moisture taking place over the same time period

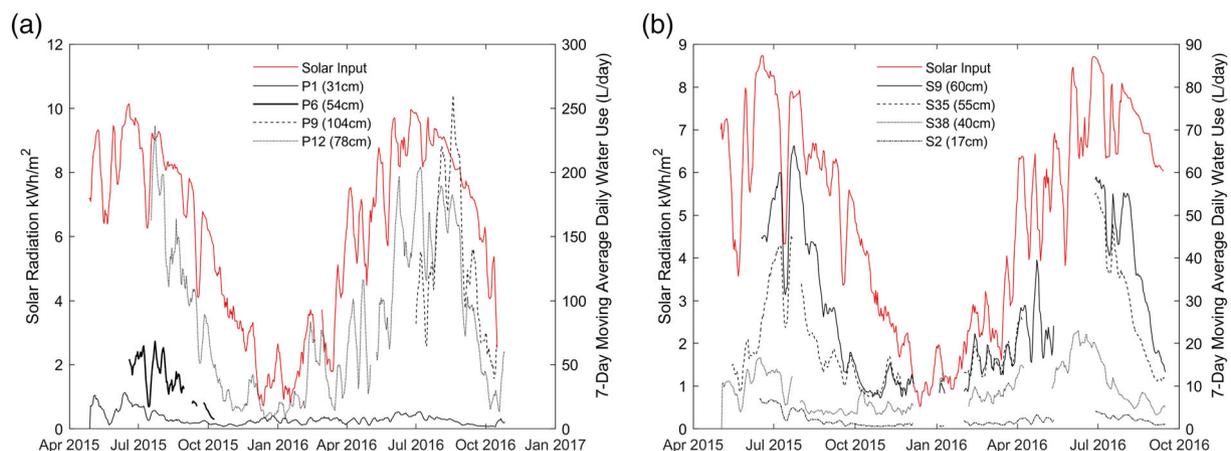
(Figures 2, 3 and 4). Solar radiation drops 50% from  $\sim 4$  kWh/m<sup>2</sup> at the summer solstice in late June to  $\sim 2$  kWh/m<sup>2</sup> in October and  $\sim 1$  kWh/m<sup>2</sup> at the winter solstice in December. An increase in soil moisture in the fall reflects the return of the rainy season. A lag between peak rainfall and soil moisture at the Schatz site may have resulted from the coarse resolution of the soil moisture data.

The linkages between solar radiation and tree water use are clearly shown in the dramatic drop visible during cloudy periods for mid-July 2015 at both sites and in numerous other time periods. Sunny periods during February, March and April 2016 result in strong responses by the trees, utilizing moisture from the winter rains, whereas sunny periods in October produce little water use, likely because of soil moisture limitation and the lower solar angle at that time of year. Spikes in water use in November at the Schatz site reflect a clear linkage to the first fall rains, as solar input was very low and continued to decline during this period.

Over the 2-year study, Douglas-fir trees at the Petrolia site ranging in size from 23 to 104.4 cm DBH had maximum (99.5th percentile) water use ranging from 19 to 332 L/day (Table 2). At the drier Schatz site, Douglas-fir ranging in size from 17- to 92-cm DBH had maximum (99.5th percentile) water use ranging from 8 to 258 L/day (Table 2).

Late spring was a peak time period for daily tree water use, with values averaged over this time period for individual trees ranging from 2 to 10 times higher than the late summer low flow values. Site average water use was 5 times higher in the spring at Schatz. Winter and early spring water use was notable. Winter tree water use ranged from 22% to 89% of peak spring water use, with a site average of 54% of peak at Petrolia and 44% at Schatz.

For the peak spring period, the drier 2015 had consistently higher tree water use as compared to 2016 at Petrolia, the wetter site. The Schatz site had higher water use in 2015 as compared to 2016 for 6 of 11 trees with complete records, with the rest being lower or equivalent. At both sites, the largest trees showed less of a reduction in water use in the dry season as compared to the smaller trees. For example, S12 at 92-cm DBH used water during the dry period at 33%



**FIGURE 2** Solar radiation and 7-day moving average daily water use for representative (a) Douglas-fir Trees, Petrolia, California, USA and (b) Douglas-fir Trees, Schatz Tree Farm, California, USA

TABLE 2 Douglas-fir daily water use

Tree	DBH (cm)	Average daily water use						
		Peak 2015 <sup>a</sup> (L/day)	Peak 2016 (L/day)	Low 2015 (L/day)	Low 2016 (L/day)	Spring 2016 (L/day)	99.5% Daily water use (L/day)	99.5% Sap velocity (cm/day)
Petrolia								
P1	32	14.7	9.8	2.8	2.7	6.3	38.2	131
P2	38	10.0	8.3	1.6	2.0	4.2	29.9	49
P3	42	11.1	11.5	5.5	5.2	7.8	33.7	53
P4	23	13.7	N/A	N/A	N/A	N/A	27.8	156
P5	43	26.4	22.9	N/A	4.9	N/A	40.6	106
P6	54	51.0	N/A	4.7	N/A	N/A	79.4	79
P7	52	10.7	6.9	5.0	3.7	6.1	19.0	29
P8	65	37.3	N/A	10.8	N/A	N/A	93.2	64
P9	104	N/A	144.1	N/A	93.1	N/A	316.0	85
P12	79	188.6	160.2	25.5	63.7	35.8	252.9	127
P14	76	264.0	167.1	56.2	97.0	51.0	332.1	145
Schatz								
S1	46	46.47	28.76	7.04	N/A	12.32	59.2	96
S2	17	6.44	4.10	0.78	0.98	1.46	7.9	59
S3	55	54.12	36.90	10.26	12.59	14.72	67.9	76
S4	43	35.65	32.48	7.78	5.78	13.55	43.2	112
S5	46	81.32	N/A	6.07	N/A	30.56	102.6	106
S7	34	18.74	12.23	1.47	N/A	N/A	27.3	74
S9	60	50.81	58.21	9.79	15.83	17.98	68.9	96
S10	64	48.67	N/A	11.40	N/A	16.42	87.0	101
S12	92	180.90	139.68	60.45	62.62	N/A	257.6	147
S33	39	28.75	28.02	3.05	4.38	10.58	35.7	76
S35	55	33.50	54.71	8.74	11.36	17.46	57.2	70
S38	40	14.09	19.74	5.83	4.19	9.00	25.3	50
S39	37	N/A	14.23	N/A	11.09	14.56	38.1	54
S40	58	17.37	N/A	7.94	N/A	N/A	22.4	31
S43	60	52.15	35.36	6.93	5.56	10.80	69.6	67

<sup>a</sup>Columns refer to average daily water use for discrete seasons. Peak 2015 occurred from 6/8/2015–7/4/2015. Peak 2016 was 6/7/2016–6/27/2016. Low 2015 was 9/26/2015–10/21/2015. Low 2016 was 8/27/2016–9/13/2016. Spring 2016 was 1/29/2016–4/13/2016.

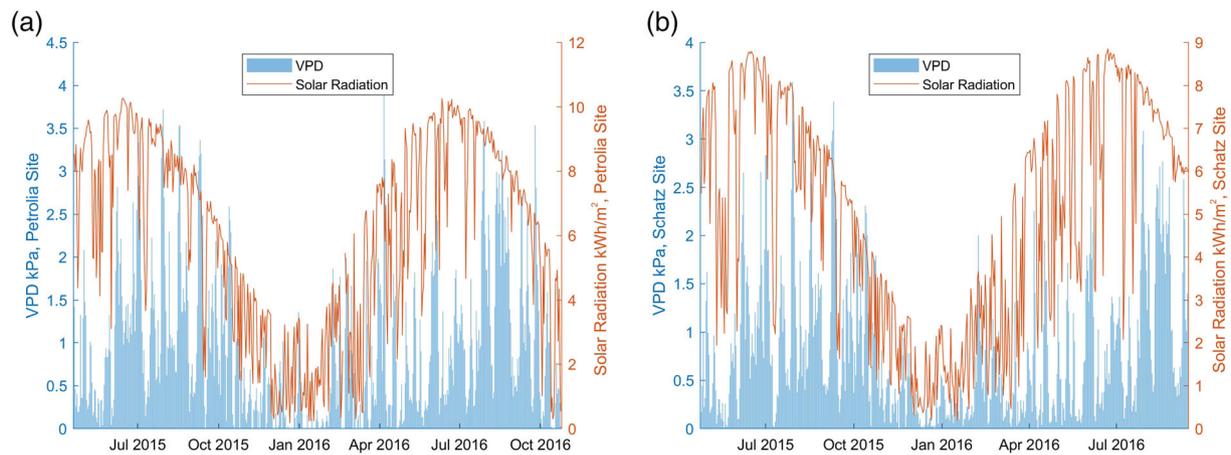
of peak spring flow rates, while S3 at 55-cm DBH was using water at 19%.

For the summer dry period, most trees at the Petrolia site had daily water use values that were roughly comparable in 2015 and 2016. However, two of the largest trees (P12 and P14 on Table 2) showed dramatically higher summer water use values in 2016. The same two had higher spring peak water use in 2015. The Schatz site showed roughly similar summer low flow values in both years, with 5 of the 10 trees with complete records showing slightly higher water use in 2016 and half slightly lower.

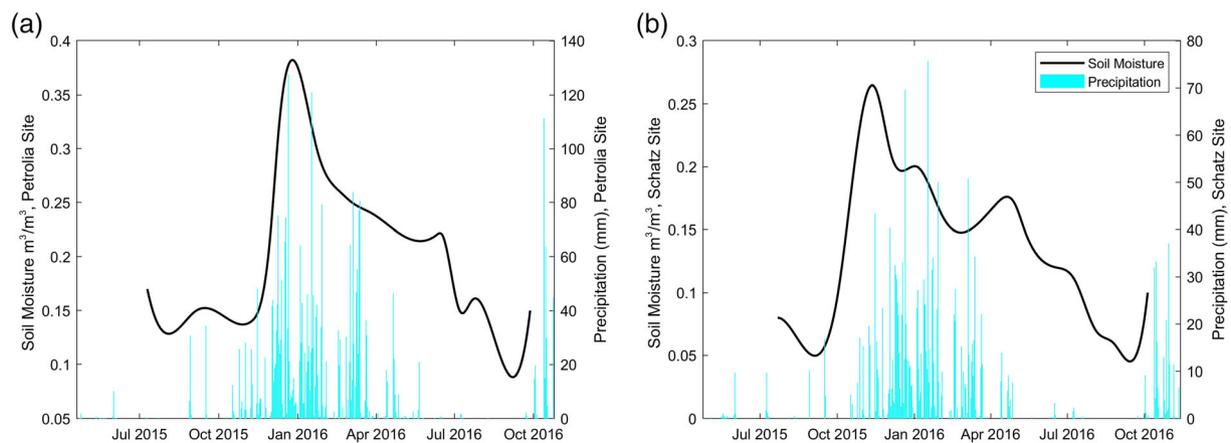
Water use is closely linked to tree diameter as shown in the figures and Table 2, with the smallest trees using considerably less water than the largest trees. Larger trees had as much as 40-fold maximal water use as compared to the smaller trees in the study.

The relationship between tree size (sapwood area) and daily water use averages was consistent for both the summer low and spring peak periods as shown in Figure 5. Regression coefficients for the more complete 2015 year were 0.692 at low flow ( $p = 0.0002$ ) and 0.809 at peak flow ( $p = 0.00001$ ) for the Schatz site. At the Petrolia site, regression coefficients for the better sampled 2015 year were 0.780 at low flow ( $p = 0.004$ ) and 0.812 at peak flow ( $p = 0.0004$ ). The Petrolia site had larger water use values, possibly reflecting a wetter site, but also the influence of larger tree sizes. Petrolia has three trees with over 1700-cm<sup>2</sup> sapwood area, while Schatz site has only 1.

The DBH of sample trees (cm) was closely related to sapwood thickness (cm). The regression equation (sap thickness =  $1.6 + 0.282$  DBH) had an  $r^2$  value of 0.89 ( $F$  statistic = 190,



**FIGURE 3** Solar radiation and vapour pressure deficit, (a) Petrolia, California, USA and (b) Schatz Tree Farm, California, USA



**FIGURE 4** Precipitation and soil moisture, (a) Petrolia, California, USA and (b) Schatz Tree Farm, California, USA

$p$  value =  $6.8 \times 10^{-13}$ ). Local density was not found to be significantly correlated with tree water use at either site.

VPD was characterized by huge variability, with peaks of several days duration (2–3.5 kPa) alternating with periods of very low VPD (0.1 kPa). Peaks were consistently high throughout summer 2015, and then dropped to very low levels with the fall rains. In Summer 2016, peaks appeared to get higher and longer in duration as the summer persisted, with days of high VPD persisting into October 2016. Daily fluctuations are observed corresponding to cloud cover and the humidity of air masses moving through. In general, higher VPD corresponds with days of higher solar radiation, although disjunctive periods are observed as well, resulting presumably from higher humidity air masses moving through.

Soil moisture collection did not begin until July of the first year. Comparing the two sites, higher soil moisture levels were observed at the rainier Petrolia site during the wet season and the higher levels persisted into the dry season. The soil moisture data do not show daily fluctuation because the data set was collected biweekly.

Linear mixed effects models of natural log of tree sap velocity were created using meteorological variables as input. A summary of

the different models evaluated is presented in Table 3. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. Random effect terms due to variation between trees, year and site were the same for all comparisons. These were modelled as intercepts. The null model consisted of the random effect terms, plus the fixed effect term date, which was number of days elapsed since 1 January of each year. The AIC scores are listed for each model. The log likelihood ratio as compared to the null model with a  $p$  value is also presented.

The best model fit (AIC:  $-6523$ ) was found for the model using solar radiation and VPD scores, followed by a model that used solar radiation alone (AIC:  $-6334$ ). The model adding soil moisture to solar radiation and VPD was third, with a notably smaller AIC score of  $-4966$ . The log likelihood scores support this ranking. Model runs that included soil moisture but not solar radiation as an input had much lower AIC scores and log likelihood results showed they did not perform better than the null model ( $p = 1$ ). VPD alone had a smaller AIC score of  $-4796$ . Model results using input variables offset by 1 day to investigate the effects of time lag (not shown) performed worse than those presented.

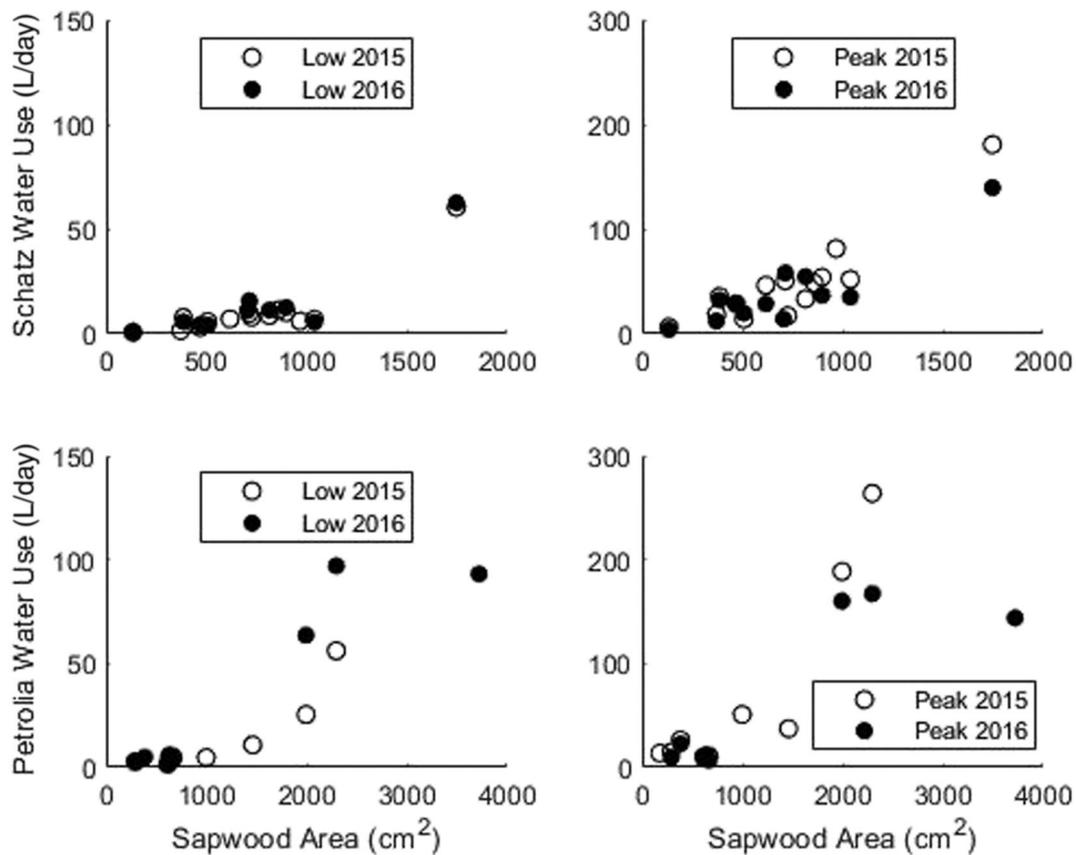


FIGURE 5 Seasonal Douglas-fir water use summaries, 2015, 2016

TABLE 3 Linear mixed effects model of Douglas-fir natural log sap velocity

Fixed effects <sup>a</sup>	Random effects	AIC <sup>b</sup>	Likelihood ratio w/ null model	<i>p</i> value
Solar + VPD + SoilM + Date	(1 Tree) + (1 Summer) + (1 Site)	-4966	699	0
Solar + SoilM + Date	(1 Tree) + (1 Summer) + (1 Site)	-4868	599	0
VPD + SoilM + Date	(1 Tree) + (1 Summer) + (1 Site)	-3754	-466	1
SoilM + Date	(1 Tree) + (1 Summer) + (1 Site)	-3588	-683	1
Solar + VPD + Date	(1 Tree) + (1 Summer) + (1 Site)	-6523	2255	0
Solar + Date	(1 Tree) + (1 Summer) + (1 Site)	-6334	2063	0
VPD + Date	(1 Tree) + (1 Summer) + (1 Site)	-4796	525	0
Null: Date	(1 Tree) + (1 Summer) + (1 Site)	-4273	-	-

<sup>a</sup>Wilkinson notation used: where 1 is intercept, name is fixed effect and (1|Name) denotes random intercept for that term. Solar is solar radiation (kWh/m<sup>2</sup>), VPD is vapour pressure deficit (kPa), SoilM is gravimetric soil moisture (m<sup>3</sup>/m<sup>3</sup>), Date is # of days since 1 January (no year) and Tree denotes intercept for random variability between trees.

<sup>b</sup>Lowest values are best model fit, for example, AIC: -6523.

Detailed coefficient estimates are shown in Table 4a for the full model (solar + VPD + soil moisture + random effect terms) and in Table 4b for the best model (solar + VPD + random effect terms). Also provided are standard deviations for coefficients, *t* test statistics, *p* values and 95% confidence intervals for the coefficients. Note that in the full model, the fixed effect coefficient for soil moisture was not significant (*p* = 0.2) and the 95% confidence interval includes zero. Other fixed effect terms were highly significant (*p* < 0.00001). The fixed effect date was very small (-0.001). The random effect terms, in

the form of intercepts, all had small but positive values, with the 95% confidence intervals for the estimates all above zero. The difference in intercepts between years (0.034), between sites (0.048), and between trees (0.091) were all fairly small compared to the intercept for the fixed effects (0.492) and the residual error of the model (0.115).

For the best model, with solar and VPD as fixed effects, coefficients were quite similar to the full model and also highly significant. Confidence intervals were slightly smaller suggesting greater

**TABLE 4** Linear mixed effects models of Douglas-fir natural log sap velocity

Name <sup>a</sup>	Estimate	SE	t stat	DF	p value	95% CI lower	95% CI upper
a. Statistics for full model: solar + VPD + soil moisture							
Fixed effects coefficients							
Intercept	0.492	0.069	7.08	3407	<0.00001	0.355	0.628
Date	-0.0011	0.0002	-6.52	3407	<0.00001	-0.0014	-0.0007
Solar	0.054	0.001	37.37	3407	<0.00001	0.051	0.057
SoilM	0.204	0.160	1.27	3407	0.20	-0.110	0.518
VPD	0.025	0.002	10.11	3407	<0.00001	0.020	0.030
Random effects covariance parameters							
Summer (2 levels)	0.034					0.011	0.108
Site (2 levels)	0.048					0.013	0.181
Tree (26 levels)	0.091					0.068	0.121
Residual Error	0.115					0.112	0.117
b. Statistics for solar and VPD model							
Fixed effects coefficients							
Intercept	0.536	0.049	10.88	4648	<0.00001	0.440	0.633
Date	-0.0012	0.0001	-23.41	4648	<0.00001	-0.0013	-0.0011
Solar	0.054	0.001	45.84	4648	<0.00001	0.052	0.056
VPD	0.032	0.002	13.99	4648	<0.00001	0.028	0.037
Random effects covariance parameters							
Summer (2 levels)	0.036					0.012	0.114
Site (2 levels)	0.052					0.016	0.171
Tree (26 levels)	0.078					0.059	0.104
Residual error	0.118					0.116	0.121

Note: SoilM is gravimetric soil moisture ( $m^3/m^3$ ), and Date is # of days since 1 January (no year). Site, Summer and Tree denote random effects intercepts. <sup>a</sup>Velocity is sapflow velocity, cm/day, Solar is solar radiation ( $kWh/m^2$ ) and VPD is vapour pressure deficit (kPa).

**TABLE 5** Statistics for solar and VPD model trained with Schatz data

Name	Estimate	SE	t stat	DF	p value	95% CI lower	95% CI upper
Fixed effects coefficients							
Intercept	2.145	0.130	16.52	2812	<0.000001	1.890	2.400
Date	-0.0037	0.0004	-10.34	2812	<0.00001	-0.0045	-0.0030
Solar	0.266	0.008	31.85	2812	<0.00001	0.249	0.282
VPD	0.053	0.018	3.00	2812	0.003	0.019	0.088
Random effects covariance parameters							
Summer (2 levels)	0.127					0.047	0.345
Residual error	0.666					0.649	0.684

precision. Again, the random effect intercepts were small compared to the fixed effect intercept and the residual error. This model was used to train the Schatz data, for validation against the Petrolia data set. Model results are shown in Table 5. Model coefficients were highly significant despite fewer data points. Again, Date was the weakest contributor, with a very small coefficient. The VPD had a smaller test statistic than other fixed effects, with a greater relative interval of 95% confidence, suggesting that the effect of this statistic was less precisely estimated (though the  $p$  value was still significant

[ $p = 0.003$ ]). The VPD coefficient was much smaller than the coefficient for solar radiation (0.053 vs. 0.266) suggesting less influence on the model. This comparison of fixed effects coefficients is valid given that both variables have similar ranges of input values (see Figure 3). Greater residual error was observed for the model when applied to one site versus both (0.666 vs. 0.115).

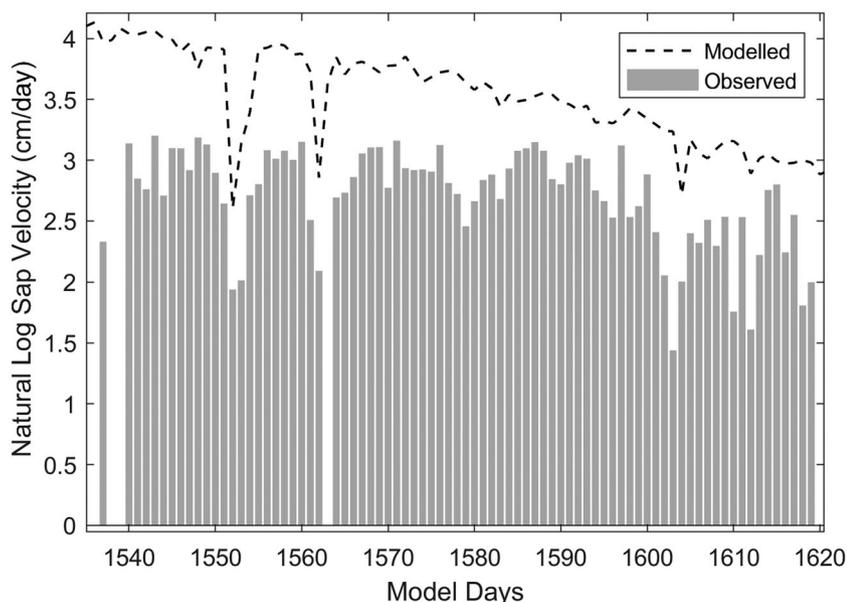
This model was then used to generate predictions for sap velocity at the Petrolia site from solar radiation and VPD inputs at that site. Model predicted sap velocities were then compared against

observations for individual trees. Representative comparisons are shown in Figures 6 and 7. The model performed well, capturing both the gradual rate of seasonal decline and weekly variations in sap velocity driven by short-term weather events. Occasional disjunctive single day events, where the model observed data show small declines not matched by the other data record, may reflect the distance that the meteorological station was from the field site. This was far enough away to show differences in short-term cloud cover, but not larger multi-day events. In comparing the model time periods, it is apparent that data for Tree 3 in Figure 6, was over-predicted ~25% in places, while data for Tree 5 in Figure 7 was underpredicted as much as 5% by the model. The PBIAS of -15.6% for all the trees at the Petrolia site suggests that underprediction was the more dominant trend. This level of bias is considered

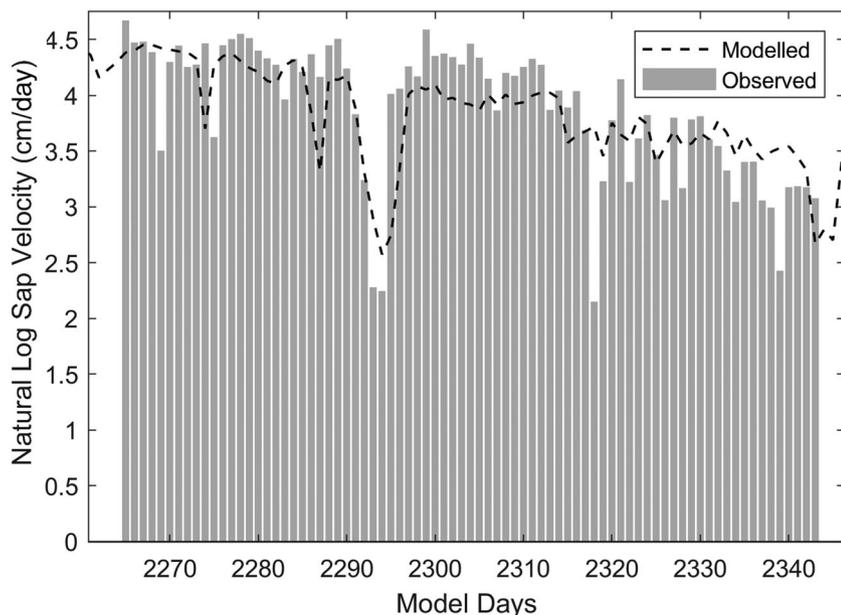
satisfactory for hydrologic models (Moriassi et al., 2007). The Nash-Sutcliffe efficiency index was 0.92. The relative error statistic was 0.28. Both values are considered a very good fit for hydrologic models (Moriassi et al., 2007).

## 4 | DISCUSSION

This study was successful in capturing daily water use values for Douglas-fir trees for discrete seasonal periods in 2015 and 2016 and developing a linear mixed effects model that predicts daily water use from commonly measured meteorological variables. The discrete seasonal periods were peak spring transpiration, late summer seasonal drought and the winter/early spring rainy period.



**FIGURE 6** Modelled versus observed sapflow velocities, Summer 2016, Tree 3, Petrolia, California, USA



**FIGURE 7** Modelled versus observed sapflow velocities, Summer 2015, Tree 5, Petrolia, California, USA

The strong seasonal decline in Douglas-fir transpiration recorded over the course of each summer supports observations made in Northern California by Link et al. (2014) on the Elk River watershed, and Stubblefield et al. (2012) in the upper Mattole River watershed. The decline in water use is important to consider in understanding how water budgets will change as oak woodlands and grasslands in this area gradually experience encroachment by Douglas-fir (Beckmann et al., 2021; Link et al., 2014) and as the forests respond to a warming climate.

If Douglas-fir is largely shutting down in late summer, the impact of a shift in forest composition to Douglas-fir may be reduced influence on soil moisture and streamflow in late summer. This depends on the extent to which the current vegetation types, oak woodland and grassland are accessing water in late summer. Ongoing investigations into oak species water use in this area will inform this question.

Another relevant factor is the extent to which spring water use affects the availability of late summer soil moisture and groundwater feeding streams. Forest cover uses more water than grassland cover (Ward & Trimble, 2003). A dense forest of Douglas-fir may reduce available soil water quickly during the peak early summer period. This has been observed, for example in oak forest (Devine & Harrington, 2007). By depleting soil moisture, the trees may influence water available for late season growth and affect late summer stream baseflows as well (Lovill et al., 2018).

Some insight into this influence on baseflow is provided from the Caspar Creek experimental watersheds (Keppeler & Ziemer, 1990). After selective harvest of 85-year-old Douglas-fir and Redwood, increases in annual stream flow and late summer flows were observed. In the 6-year post-harvest, summer flow volumes increased by 29% and the number of low flow days (below 5.66 L/s) decreased by 40%. While the summer flows showed a larger proportional increase relative to annual flows, the majority of the observed increase, 90%, was observed in the winter and spring. Mountainous watersheds typically have minimal groundwater storage, limiting the potential carry over of additional water yield from reduced evapotranspiration during the wet season to the dry.

Another factor to be considered is the effect on stand-level water use of the composition of a forest stand with respect to size of individuals and forest density. This study found dramatically larger water use for larger trees, with the increase being out of proportion with the increase in sapwood area. Furthermore, the larger trees maintained significant water use for longer into the dry period. This suggests that the largest trees have accessed a more reliable water source, through deeper roots, or position on the landscape. However, an older forest, due to canopy closure and disturbance, has fewer trees per hectare. A forest growth model of these factors (Stubblefield et al., 2012) over time suggests that older forest may use less water than younger stands. Moore et al. (2004) also report greater water use in younger stands.

This study did not find significant correlations between local density, a measure of competition and tree water use. This may be a result of small sample size, and the fact that shading was not explicitly evaluated. Further evaluation of size and effects of inter- and intra-

species competition for water and sunlight on water use would necessitate a larger study with sites in a range of forest compositions. A recent study in the region (Beckmann et al., 2021) found strong competitive effects of encroaching Douglas-fir on Oregon white oak, using annual growth increment from tree cores. This finding indicates competitive effects on tree water use should be expected.

While California was just ending a historical multi-year drought in 2015, annual rainfall in the northern coastal region was not too far below long-term averages. Rainfall was above average in 2016. Indeed, higher water use was recorded in 2015 than 2016 for some trees at both sites. This suggests that at Petrolia, the dry 2015 year was not dry enough to limit tree growth significantly in the spring. More water in 2016 did not cause more water use. This may result from the dryer 2015 having more sunshine to drive tree growth and water use.

For the late summer dry period, trees at the Petrolia site were fairly similar between years. For 2015, the trees that had higher spring water use in comparison to 2016 showed lower late summer water use in comparison to 2016. Essentially, the drier 2015 provided more sunshine for spring transpiration, but less water for late season transpiration. In 2016, more water was available to these trees in the late summer.

Trees at the Schatz site during the dry period were also similar between years. Two factors might explain the lack of difference between wet and dry years at the drier Schatz site. First, the summer dry period is part of the Mediterranean climate. Both years were dry enough by that point in the summer to significantly shut down Douglas-fir water use, regardless of differences in winter and spring precipitation. Another factor was the vegetative response to the recent thinning treatments. A very strong understory response to the thinning was observed in Summer 2016, and that may have resulted in competition for soil moisture with monitored trees. In Summer 2015, the thinning had just taken place, and so there was less competition for water from overstory trees and understory shrubs.

The linear mixed effects modelling provides insight into driving factors of daily tree water use as well as a specific equation that can be used to predict water use for Douglas-fir trees. The results of linear mixed effects modelling show a strong role for solar radiation as a driver of daily water use and a weaker role for VPD and soil moisture.

We had expected a stronger role in the model for soil moisture. It is generally considered to be the cause of the seasonal decline in tree water use in Mediterranean climates such as this one. The importance of soil moisture is apparent by the reinvigoration of tree water use observed in the early fall when the first rains occur. It is also relevant to consider that during the winter, when solar radiation is low but soils are wet, Douglas-fir water use is still quite notable (Figures 2 and 3).

Several reasons likely explain why the model was not strongly driven by soil moisture. While soils are drying out in late summer, the available solar radiation is also declining steeply, particularly in regions of higher latitude. Because of the co-occurring decrease in solar radiation, little further information is provided to the model from the steadily declining soil moisture. However, day to day variability in

solar radiation, from cloudiness, greatly explains daily drops in transpiration, as observed in Figures 2 and 3. Furthermore, it is likely that in the spring, soil moisture is not limiting, and so less relevant to tree water use. All of these factors mean that the model focusing on solar radiation provided a stronger predictive effect. If we were to perform the experiment for 10 years of varying rainfall and soil moisture, it is logical that a model utilizing soil moisture would be best at predicting seasonal water use. This experiment has essentially been run in studies of tree ring width and annual rainfall, where tree ring annual increment is representative of tree water use (e.g., Henttonen et al., 2014).

A higher resolution soil moisture data might have resulted in greater predictive effect for this variable in the model. More recent high-resolution measurements of soil moisture in a nearby location (unpublished data of the authors, 60-min interval, summer 2018 and 2019), also show a gradual decline in soil moisture over weeks. A slight diurnal sine wave pattern (range: 1%–2% of water content) is visible in this data, with a late afternoon low point and a midnight high point. This reflects drying and rewetting in response to transpiration demands from the roots and soil evaporation.

VPD was also not as strong a driver in the model as solar radiation. This may reflect limitation by soil moisture in late summer, so even though VPD is high, the trees are unable to respond because water is not available. VPD may remain sufficiently high in the summer season that day to day variations are not important drivers of tree water use. Link et al. (2014) found that Douglas-fir water use was more sensitive to VPD changes during the winter than the summer. Bond et al. (2007) describe a saturating response to VPD, where tree water use stops responding to increasing VPD after a certain point. The mechanism is thought to be leaf stomatal conductance, lowered by the tree to limit cavitation. Link et al. (2014) note that tree water use responses to variables that are nonlinear, threshold-sensitive or interactive are not well captured by linear models.

The test of the linear mixed effects model developed on one site, to predict sapflow velocity for a second site, was successful. Solar radiation and VPD (or its components of temperature and humidity) are widely available from the RAWs network, making it possible to use these coefficients to estimate water use for other locations. To accomplish this, daily solar and VPD data would be input into the model along with Julian date since the beginning of the calendar year. The resulting raw sapflow velocity values reflect the transformations that were performed. Thus, to calculate actual water use values, the following equation should be used:

$$T = SA * e^{v * v_{max}} \quad (4)$$

where  $T$  is transpiration or daily water use (cm/day),  $SA$  is the sapwood area of the tree (cm<sup>2</sup>),  $e$  is Euler's number,  $v$  is the sap velocity from the model output (dimensionless) and  $v_{max}$  is the 99.5th percentile daily integral sapflow velocity (cm/day). Sapwood area could be measured by coring the tree to determine sapwood thickness, or could be estimated from DBH, using the regression relationship between  $SA$  thickness and DBH observed here, or in other studies (Link et al., 2014 and Smith et al., 1966). We did not observe a linear

relationship between  $v_{max}$  and DBH or  $v_{max}$  and  $SA$ . We recommend using an average of the measured values for  $v_{max}$ . For the combined sites, we recorded an average  $v_{max}$  of 86 cm/day, with a standard deviation of 35 cm/day. Link et al. (2014) also report a range of 99.5th percentile daily integral sapflow velocities for Douglas-fir trees.

Sources of error include variability in sap velocity between trees, and errors from the model fit. The model showed a –15.6% PBIAS, suggesting estimated water use values would be slightly underestimated. For many applications however, this level of accuracy would be quite informative and comparable to levels of error measured for other methods of estimating transpiration.

## 5 | CONCLUSIONS

We have obtained water use data for Douglas-fir growing in northern coastal California and developed and evaluated predictive models that use environmental variables to predict water use. This work may be used to inform regional water balance calculations and models used to that inform forest management, water supply and aquatic species recovery efforts. Furthermore, it is relevant for ongoing efforts to evaluate the impact of Douglas-fir encroachment in loss of oak woodlands (Beckmann et al., 2021).

Douglas-fir trees used a wide range of water (8–332 L/day). Sapwood area was correlated with daily water use averages for both peak and low periods. DBH was closely related to sapwood thickness. Peak water use occurred in June and July, dropping dramatically to lows recorded in August through September. Peak values were 2–10 times higher than low flow values. Winter water use was notable, continuing at 44%–54% of peak water use on average. Thus, the impact of Douglas-fir encroachment, and/or high stand densities on dry season water supplies and river low flows may be minimal in late summer, or a carryover effect of increased winter and spring water use.

The first year of the study, 2015, was drier than the second, 2016. Peak season water use at the Petrolia site was greater in 2015. This may result from more clear days and less fog, resulting in more solar radiation to drive transpiration and thus water use. Low season water use was comparable between year for most trees. However, for two of the largest trees, greater dry season water use was observed in 2016. The implication is that the effect of drought years is most impactful during the driest time of year, with less water carrying over from the wet season. At the Schatz site, no clear differences emerged between years. This may reflect adequate moisture in both years for optimum water use in the spring peak period and limitation by similar soil moisture levels in the summer low period. Vigorous understory growth in 2016 after the 2014 thinning may have provided competition with the trees for soil moisture, thus preventing an increased water use response in study trees to the wetter year. It is important to note that the sites are in the southern extent of the Douglas-fir range. More northerly sites would be expected to have more evenly distributed rainfall and fewer periods of water stress.

Study trees appear to be light limited during the wet spring periods, responding directly to solar radiation variability, and water limited during the late summer dry periods, showing little variability with solar radiation, and immediate increases in water use with the first fall rains. Local density, a measure of the density of competing trees within a 6-m radius, did not appear to affect tree water use. We recommend future studies incorporate spatial mapping of shading and crown position to inform impact assessment of competition.

Higher VPD corresponded with days of higher solar radiation, although some periods of high humidity and sunshine were observed. Soil moisture declined steadily over the summer. Higher soil moisture was observed at the rainier Petrolia site and this difference persisted into the summer.

Linear mixed models were developed to evaluate driving environmental variables and to create a tool for prediction of Douglas-fir water use. Solar radiation and VPD were highly significant coefficients in the model, with solar radiation being the most influential driving variable. Soil moisture was not a significant variable. This may result from autocorrelation between declining day length and soil moisture over the late summer, and the dependency of soil moisture drying rate on solar radiation.

The model was tested by calibration with Schatz site data and then using it to predict values recorded for the Petrolia site. Model coefficients were highly significant, and VPD appeared to have less influence on model output. Statistical measurements (PBIAS, Nash–Sutcliffe efficiency index and relative error statistic) indicated a very good model fit to the data, with some underprediction occurring. Model coefficients and an equation to convert sap velocity to water use values are provided.

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in a digital repository at this address: <https://doi.org/10.5281/zenodo.4895151>.

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