AN EXAMINATION OF WATER CONSUMPTION DURING AND AFTER SEVERE DROUGHT IN COASTAL STANDS OF DOUGLAS-FIR IN THE PACIFIC NORTHWEST

By

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ABSTRACT

AN EXAMINATION OF WATER CONSUMPTION DURING AND AFTER SEVERE DROUGHT IN COASTAL STANDS OF DOUGLAS-FIR IN THE PACIFIC NORTHWEST

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The Pacific Northwest region is predicted to encounter rising temperatures over the next century, ultimately leading to less water storage during seasonal drought periods. Vast coniferous forests dependent upon this storage and will encounter periods of increased stress due to the lessening of available water supply. Under these conditions, stream flows will be directly affected by the forests competing for freshwater sources. Thinning treatments have been investigated as a means to compensate for increased water use by even-aged forest stands left over from past logging-practices.

This study was completed on two sites within Humboldt County, CA: one inland site with a relatively dry climate and one coastal site with a wetter climate. Thinning treatments were implemented at the dry site in fall of 2014, while the wet site underwent thinning treatments in 2009. For this study, eight sample Douglas-fir trees were chosen at each site representing various sizes and levels of competition. Sap flow measurements were taken during the summer drought period in 2015 and 2016. Water use was compared between trees, sites, and sample periods, with a focus on the differences between 2015, the fourth year in a 4-year drought, and 2016, an exceptionally wet year. Patterns of water use were strongly affected by the drought, manifested as high nighttime water use due to cavitation and increased dependency on bole water storage. Adaptive water use strategies of the old-growth sample tree (diameter at breast height (DBH) = 104 cm) and increased water allocated to sample trees receiving more solar radiation were observed as well. Despite an above average annual precipitation in 2016, increased water stress was evident at the dry site, likely due to understory regeneration following thinning treatments and increased growth characteristic of a re-watering year. DBH was positively correlated with water use during the lower stress 2016 growing season, while poorly correlated during preceding season of high stress, signifying that other factors may play a more important role when assessing water use during times of low water availability. Local competition was not found to significantly influence tree water use.

ACKNOWLEDGEMENTS

I would like thank my advisor, Dr. Andrew Stubblefield, for all of his help and encouragement throughout the past three years. I would also like to thank my committee for all of the time spent giving me constructive criticism on this paper, as well as Dr. Aaron Hohl for helping with individual tree measurements, site maps, and equipment installations. Thank you to the property owners of the two sites used in this study, Dr. John Williams and Gordon Schatz. Thank you to the L.W. Schatz Demonstration Tree Farm for providing funding for this project. Thank you to everyone else who has helped in so many ways, whether volunteering to help install equipment or providing advice on methods.

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INTRODUCTION

Once an intact old-growth ecosystem, the landscape of the Pacific Northwest (PNW) has experienced many changes since European settlement. Douglas-fir (*Pseudotsuga menziesii*) is one of the most prominent species that comprise the dominantly coniferous forests of this region (Halpern and Spies, 1995). Clear-cutting has been the primary means of harvesting, which has led to the replacement of old-growth forests, or virgin stands that have reached maturity, with dominantly younger, denser forest stands (Palais et al., 1950; Harr, 1976; Krankina et al.2012). Compared to old-growth forests, this young, dense forest structure uses more water (Moore et al., 2004), and therefore, likely yields less water to the watershed.

Conifers typically increase sapwood, root, and leaf area growth in response to increased water availability following thinning treatments (Black et al.1980, Morikawa et al. 1986, Aussenac and Granier 1988, Shelburne et al. 1993). Decreased among-tree competition increases soil water availability and ultimately growth in residual trees. Although opening the canopy through thinning initially increases soil water evaporation, this water loss is typically less than the amount of water gained via increased throughfall precipitation and decreased competition such that per tree water availability increases (Morikawa et al., 1986). While water yield to streams can increase directly after harvest (Stednick, 1996; Troendle, 1983; Bosch and Hewlett, 1982), this increase declines as forests regenerate due to the relatively high sapwood area associated with young growth and the acceleration of understory growth from reduced competition and increased solar radiation (Lesch and Scott, 1997; Bosch and Hewlett, 1982). Although this new regeneration can recover the pre-thinning water balance in the years directly following treatment (Aussenac and Granier, 1988), stand water use is expected to decrease overall once an uneven-aged growth structure is established.

The correlation between sap flow rates and water yield has proven to be the primary means of measuring the efficiency of forests in water production (Stednick, 1996). This correlation reflects how much water individual trees or forest stands consume, and therefore, how much water is able to enter the water table. Measuring sap flow by the heat pulse method is a reliable technique to gauge tree water consumption (Marshall, 1958; Grainier, 1986). As sapwood area size and shape vary, accurate measurement of sapwood area is integral to obtain sound sap flow values. Water yield, a reflection of the amount of water available within the soil profile of a watershed, can be gauged by soil moisture content and stream discharge.

Species, age, and size of trees are major factors in estimating water use. Compared to hardwood, coniferous forests tend to have the greatest response to thinning treatments on water yield (Bosch and Hewlett, 1981). In an unmanaged ecosystem, forests undergo succession until eventually natural death and regeneration of trees are in a stable state and stands are characterized by a low-density mixture of tree ages making up an old-growth forest structure. Old-growth forests likely yield significantly more water than younger forests primarily due to lower sapwood basal area (Vertessy et al., 2001; Moore et al., 2004). Despite the greater basal area characteristic of older and larger trees, the ratio of active sapwood basal area to inactive heartwood area is greater in younger trees. Because sapwood is the portion of the basal area that transports water (Reyes-Garcia et al., 2012), younger trees use more water per stem. Taking into account these characteristics, and the historically dominant practice of clear-cutting, the PNW is home to vast areas of young forest stands that presumably consume high amounts of water.   Based on these trends, implementing thinning treatments to encourage old-growth structure could increase potential for higher water yields.

If climate predictions are correct, spatial distribution and timing of precipitation over the next century in the PNW will lead to lower soil water availability. This decrease in soil water availability will also be in part due to increased evaporation and sap flow in response to predicted warmer temperatures and longer growing seasons (Juice et al. 2016, Mote and Salathe Jr. 2010, Mote et al. 2003). Sap flow rates are positively correlated to solar radiation, as is evident in the typical diurnal pattern of sap flow (Cermak et al. 2007). Higher sap flow rates tend to exist in trees oriented on slopes facing the path of the sun, on south-facing aspects in the Northern Hemisphere and on north-facing aspects in the Southern Hemisphere (Chirino et al. 2011). However, there is little research on how tree and stand spatial distribution influence stand water consumption and spatial distribution is seldom brought into water balance models (Kostner et al., 1998).

Increasing temperatures will also most likely increase the danger of cavitation and embolism in PNW coniferous forests. Cavitation and embolism, the formation of gaseous cavities in water conducting xylem tissue due to excessively high water tension, reduce tree hydraulic capacity (Tyree and Sperry, 1989). In Douglas-fir, and many other tall tree species, vulnerability to cavitation increases with age and size, due to increased height-related hydrostatic tension (Domec and Gartner, 2001). In response to high cavitation rates, large old trees can shift to bole-stored water use rather than soil water during the day; depending on the amount of basal area attributed to large old trees within a stand, this could potentially affect forest water balance. With temperatures in this region predicted to warm over the next century (Mote et al., 2003), it is vital that we understand how periods of drought and recovery could influence basic forest water use trends.

The purpose of this study is to explore how local density, tree size, and spatial distribution affect Douglas-fir water use in the coastal PNW during and after severe drought. As declining stream flows over the last century are likely attributable, at least in part, to widespread young dense forests typical of post-European settlement (Luce and Holden, 2009), restoration efforts in these even-aged stands will likely increase. Thus, there is a need to understand the effects of restoration on forest water balance during the regeneration period, a period with potentially higher water use due to higher sapwood areas, following these extensive landscape-scale treatments. The specific objectives of the study were to:

1. Compare water use between old and young trees under seasonal and long-term drought conditions.
2. Compare tree water use in wet and dry sites under seasonal and long-term drought conditions.
3. Determine if neighborhood density significantly influences the amount and timing of tree water use.

4. Evaluate how thinning treatments influence water use during and after drought.

California has recently experienced its most severe drought on record, lasting from the fall of 2011 through the 2015 water year. 2016 was considered a re-watering year, having received above average precipitation in the northern regions where most water storage originates for the rest of the state (Hanek et al., 2015). This study was conducted during the summer seasonal drought periods of 2015 and 2016, providing an opportunity to evaluate the effects of a critical long-term water shortage on coniferous forest stands in northern California. We expect to find evidence of drought stress at both sites during the 2015 sample period, and signs of stress relief in the following re-watering year.

MATERIALS AND METHODS

To meet these objectives, sap flow rates of Douglas-fir trees of varying sizes (with DBHs' ranging from 17 to 104 cm), as well as local and stand densities were measured at two locations in the summer of 2015 and the spring and summer of 2016. This study was performed on two sites in Humboldt County, northern California, USA.; the L.W. Schatz Demonstration Tree Farm in northern Humboldt County and on private land near Petrolia in southwestern Humboldt County. The inland 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. Although both basins have a Mediterranean climate with cool rainy winters and hot dry summers, the Mattole River watershed receives higher annual rainfall and has greater fog influence. For this reason, we refer to the inland L.W. Schatz Demonstration Tree Farm site as the dry site and the coastal Petrolia site as the wet site.

The wet site is located at 40°28'63.3198" N 124°30'75.233" W (Figure 1). The stand sampled is at a northwest aspect (28 degrees) 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 (USDA). In the 2015 water year, 138.68 cm of precipitation fell in this region, compared to 243.99 cm over the 2016 water year. The mean precipitation over a given water year for this region is about 190.5 cm (NOAA)). Temperature and precipitation data were obtained from a station in Honeydew, Ca, located about 16.5 km away from the wet site.

The dry site is located at 40°77’11.09” N 123°86’90.81” W (Figure 1). The stand sampled is at a northwest aspect (14 degrees) and also at 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 (USDA). Over the 2015 water year, 119.23 cm of precipitation fell in this region, while 162.2 fell over the 2016 water year. The average rainfall for this area is about 137.16 cm (NOAA). Temperature and precipitation data was collected from a station in Blue Lake, Ca, located about 10.5 km away from the dry site.

The dry site was experimentally thinned with variable density rentention (VDR) treatments in fall of 2014. Treatments thinned high-density young stands to accelerate pre-European forest structure, reduce stand density, increase water dividends, reduce fire risk, and promote growth and drought resilience in remaining trees. Across six 0.1 ac plots, basal area retention ranged from 15% to 45%; two control plots (0.1 ac) were left at 100% retention (Figure 2). After treatment, the site was reforested with Douglas-fir and coast redwood (*Sequoia sempervirens)* saplings in the spring of 2015. Although thinning treatments were implemented at the wet site in 2009, the local densities (within 6 meters of basal area) are still greater than the control plots’ basal areas at the dry site.

At each study site, eight sample trees were chosen to represent a wide range of sizes and neighborhood competition levels. The trees available for selection were limited by the length of cord running from tree to data logger, allowing for a maximum distance of 100 feet from centrally placed data loggers. Design of the variable density thinning experiment at the dry site also influenced which trees were chosen in an effort to sample trees under varying levels of local competition.

The sap flow method using thermal dissipation probes was used to record sap flow velocities and quantify water consumption (Granier, 1985, 1986, Lu et al., 2004). This method has been tested and verified against other techniques (Lu et al., 2004). Two holes were drilled into each sample tree through the xylem tissue after the bark was cleared away from the immediate area. 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. The differences in temperatures give corresponding sap flow rates (Davis et al. 2012). Three sample periods were chosen for comparison. From the total collected data, three sample periods were chosen for comparison. The first two periods, the summers (July 23rd through September 13th) of 2015 and 2016, were the primary focus in exploring the relationship between tree water use and drought, with additional analysis of a third period (March 1st to April 5th, 2016) to capture wet season trends.

One breast height (1.37 m) core was taken from each sample tree using an increment borer. From these cores, estimates of sapwood thickness were made visually by inspecting the wood laid over a light source; translucent wood was deemed sapwood and opaque sections were deemed bark or heartwood. Quantitative descriptions (based off metric measurements) of evenness of sapwood thickness taken from the stumps of trees cleared from the thinned plots indicated that the sapwood areas were uniform. From this observation, we concluded that one core sample was sufficient for estimating total cross sectional sapwood area. 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:

$$SA = \pi(Rt^2 - Rh^2) \qquad (1)$$

where *SA* is sapwood area, *Rt* is tree radius (without bark), and *Rh* is heartwood radius. An index of tree vigor (TVI) was calculated as the ratio of total basal area over sapwood area for each sample tree to evaluate tree vitality, where a greater TVI is generally associated with increased resilience (Oren et al., 1985).

Probe pairs (heated and reference; Dynamax, Houston, TX), were installed on the north side of each sample tree. Probes were then connected to centrally located data loggers with wire cables. To control against external forces, thermal shielding was installed and heating elements were turned off for a 48-hour period to ensure that sunlight was not influencing probe temperature readings. Temperature readings were taken every 60 seconds and recorded by Campbell Scientific (Logan, UT) CR1000 data loggers every 30 minutes throughout each sample period.

Average sap flow velocity V (cm s^{-1}) was calculated as follows:

$$V = 0.0119 * K^{1.231} \qquad (2)$$

where the dimensionless parameter K is calculated as:

$$K = (\Delta Tm - \Delta T)/\Delta T \qquad (3)$$

and ΔT is the measured difference in temperature (°C) between the heated probe and the reference probe and ΔTm is the maximum value of ΔT when sap flow is zero within a 24-hour period. Sap flow velocity is converted to sap flow rate (cm^3 s^{-1}) by multiplying V by tree sapwood area. The sap flow rate was then calculated by summing rates over the sampling period. Daily averages and seasonal sums were then made from these readings. Finally, sap flux density (liters/cm^2/day) was calculated by dividing sap flow (liters/day) by sapwood basal area (cm^2).

Monthly soil moisture levels were collected by gravimetric soil sampling methods (DeAngelis, 2007) performed by weighing soil samples before and after drying. The samples were taken at roughly 15 cm depth by hand in the field at random locations, but always at three different elevations within the study sites. At the dry site, sample collection location fell within three of the VDR plots (Figure 2). At the wet site, designated areas for random sample collections were associated with landmarks. Soil moisture probes were also installed, but due to technical difficulties there was insufficient data for analysis.

During the summer sample period of 2016, stream discharge estimations were made using the mechanical current-meter method (USGS, 2016) at the closest stream to each plot. Measurements were taken in Maple creek, the watershed of the dry site, and Mill Creek, the watershed of the wet site, (Figure 1). Weather data, including precipitation and temperature, was obtained from local weather stations (Honeydew 1 SW, CA; Blue Lake 0.6 NNW, CA) for the duration of each sample period.

At the dry site, total coniferous cover was calculated within each VDR plot before and after thinning treatments. At both the dry and wet site, total basal area was calculated within the surrounding area of each sample tree at variable distances of 6 meters. This distance was deemed to encompass roots from neighboring Douglas-fir trees competing for the same water within the soil profile (Mauer and Palatova, 2012), and therefore, an appropriate reflection of local density. The results are presented in Table 6.

Nighttime sap flow was distinguished from daytime sap flow by summing all sap flow recordings between sunset and sunrise. Timing of sunrise and sunset changed throughout the sample periods and was determined by the Julian Day and geographical coordinates of the study sites (US Naval Observatory, 2016). The percentage of nighttime sap flow was found as the percentage of nocturnal sap flow out of the entire 24-hour day (Phillips et al., 2010). Finally, the timing of the peak sap flow rate relative to the first and last day of the summer sampling period was determined for each sample tree.

Regression equations were developed between seasonal water use, DBH, and sapwood area. Multi-regression linear models were run (R Studio, version 3.4.2) in order to highlight any significant trends and relationships between sap flux, tree characteristics, and stand characteristics. Comparisons were made using paired t-tests and ANOVA.

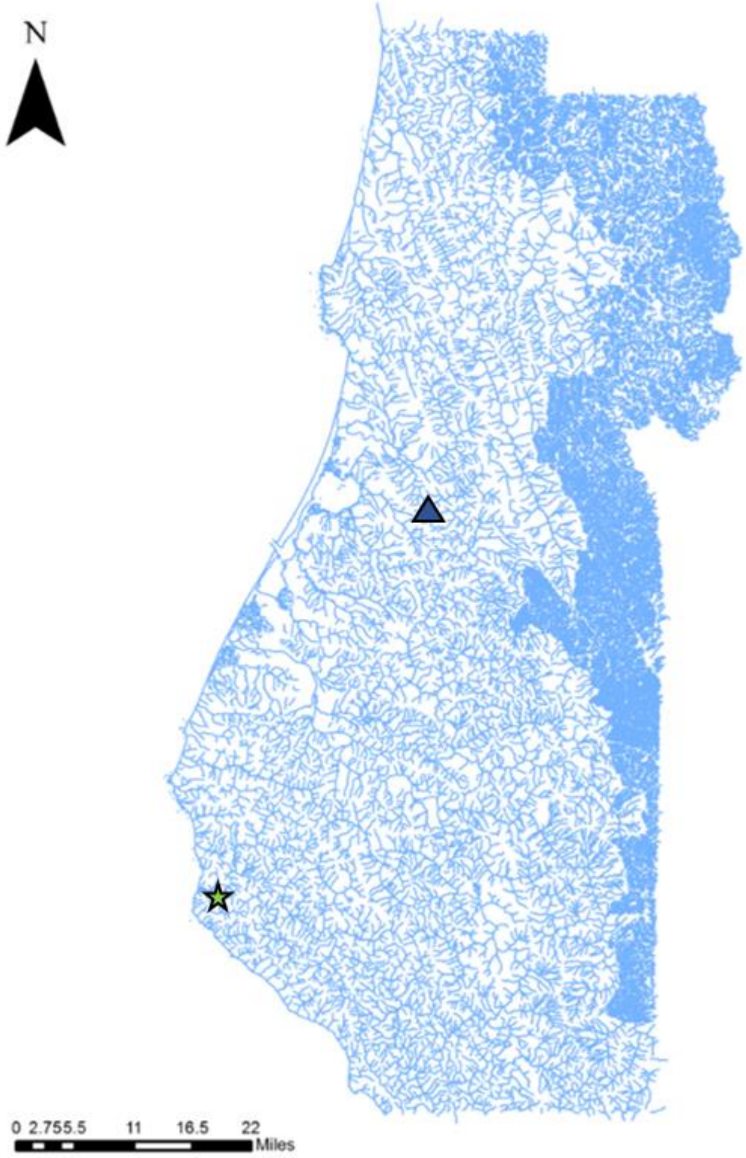

Figure 1. Map of Humboldt County, California. The triangle indicates the location of the dry site and the star indicates the location of the wet site.

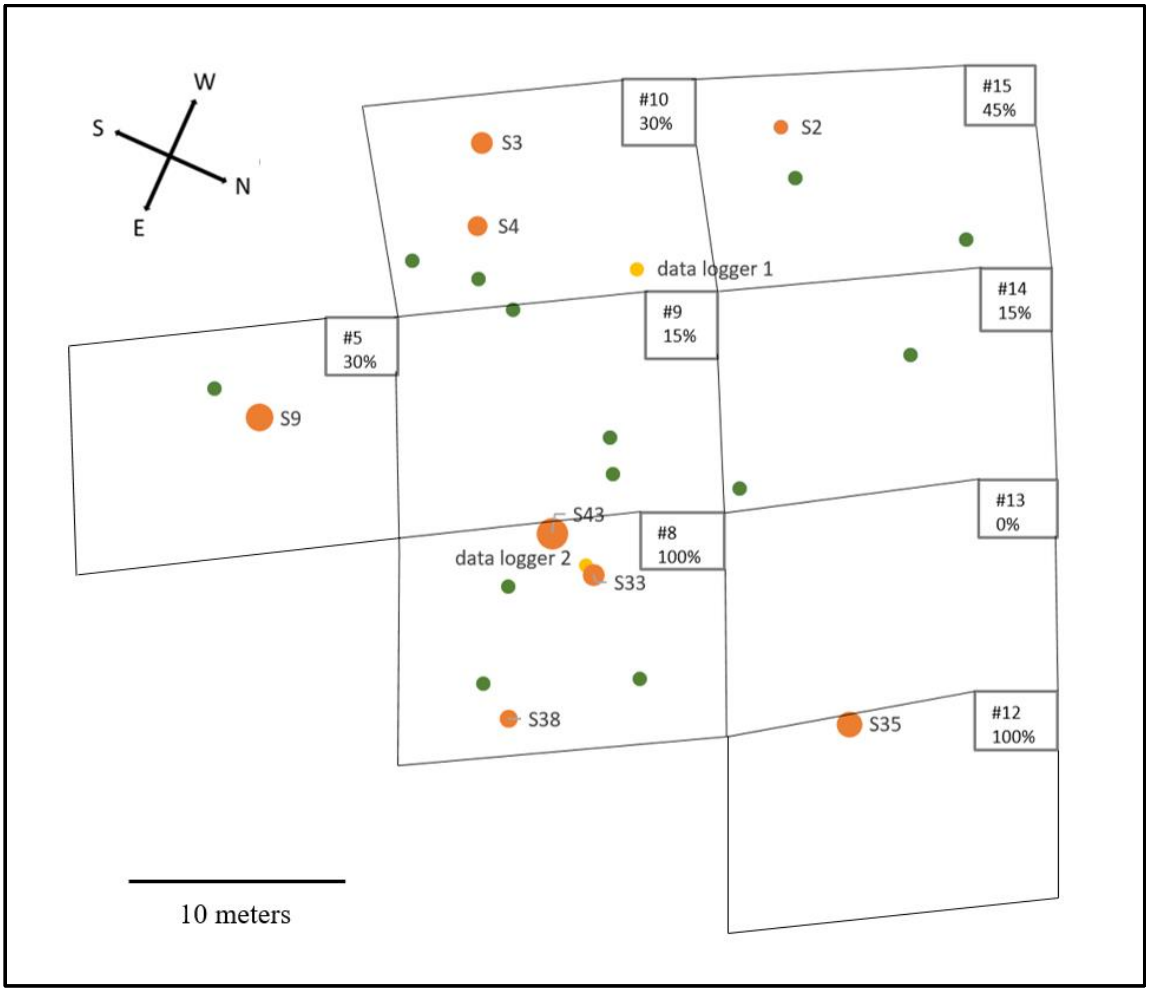

Figure 2. Map of the dry study site located in Maple Creek, California, showing the locations of each sample tree, as well as other trees within each plot. The orange dots represent the sample trees and are sized by order of DBH, while the green dots represent other trees within study plots and are not sized according to DBH. Plot number and level of variable density retention are listed within each corresponding plot.

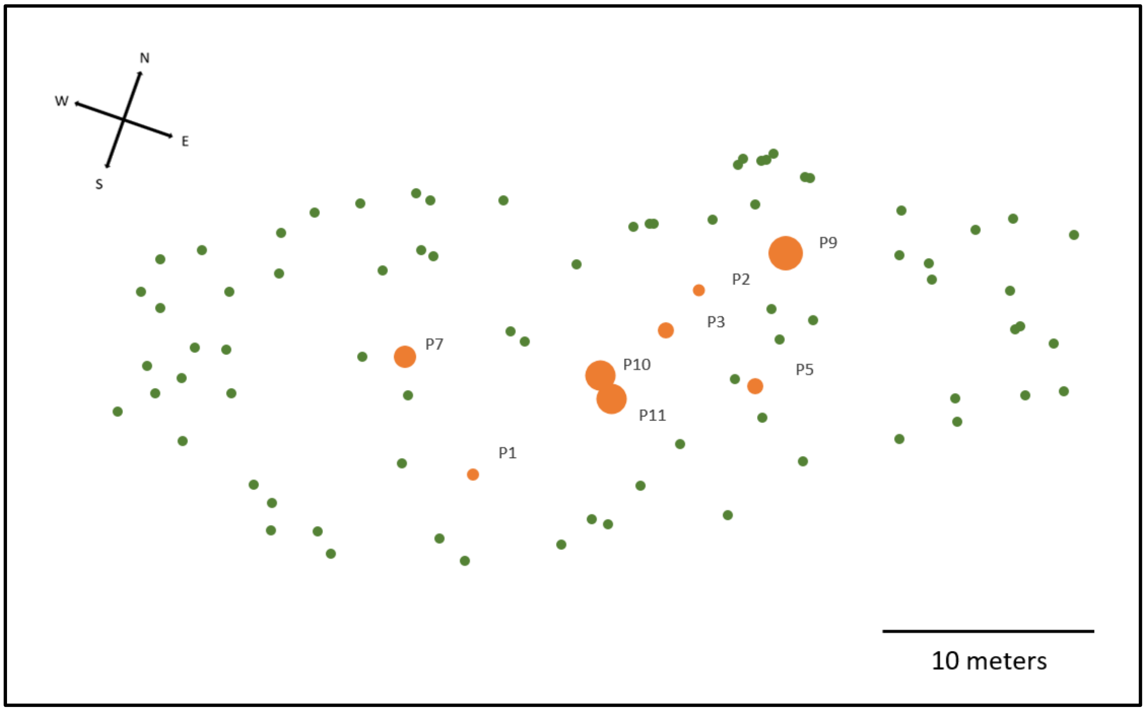

Figure 3. Map of the wet study site located in Petrolia, California, showing the locations of each sample tree, as well as neighboring trees within the plot. The orange dots represent the sample trees and are sized by order of DBH, while the green dots represent other trees within study plot and are not sized according to DBH.

RESULTS

Tree characteristics

Stem diameters (DBH) ranged from 17 to 104 cm for all sample trees at both sites, with a mean of 52 cm. The range was much smaller for the dry site (17 to 61 cm) compared to the wet site (32 to 104 cm). Mean stem diameter (46 cm) was also smaller for the dry site compared to the wet site (59 cm). Stem diameter was a good predictor of sapwood area (Figure 4, $R^2 = 0.92$, $p < 0.0001$).

Due to the exponential relationship between stem diameter and sapwood area, the mean sapwood area of the wet site (1326 cm^2) was more than twice that of the dry site (620 cm^2), despite the mean stem diameter being only about 20% greater at the wet site. Mean basal area for the wet site (3142 cm^2) was nearly twice that of the dry site (1820 cm^2). Although the mean tree vigor index (TVI; ratio of basal area to sapwood area) was greater for the dry site (2.84) compared to the wet site (2.57) TVI ranges were very similar for both sites.

Table 1. Individual tree characteristics, including DBH, sapwood area (SA), basal area (BA), and tree index (BA/SA) for all sample trees from both sites in Humboldt County, California.

Sample Tree	**DBH (cm)**	**SA (cm^2)**	**BA (cm^2)**	**Tree Vigor Index (BA/SA)**
Drier Site:				
S2	17	134	227	1.7
S33	39	469	1217	2.6
S38	40	508	1249	2.5
S4	43	386	1447	3.8
S3	55	898	2364	2.6
S35	55	815	2386	2.9
S9	60	715	2798	3.9
S43	60	1039	2870	2.8
Mean	***46***	***620***	***1820***	***2.8***
Wetter Site:				
P1	32	291	779	2.7
P2	38	615	1110	1.8
P3	42	636	1380	2.2
P5	43	384	1482	3.9
P7	52	668	2150	3.2
P9	104	3721	8559	2.3
P10	78	1994	4838	2.4
P11	78	2297	4838	2.1
Mean	***59***	***1326***	***3142***	***2.6***
2-Site Mean	***52***	***973***	***2481***	***2.7***

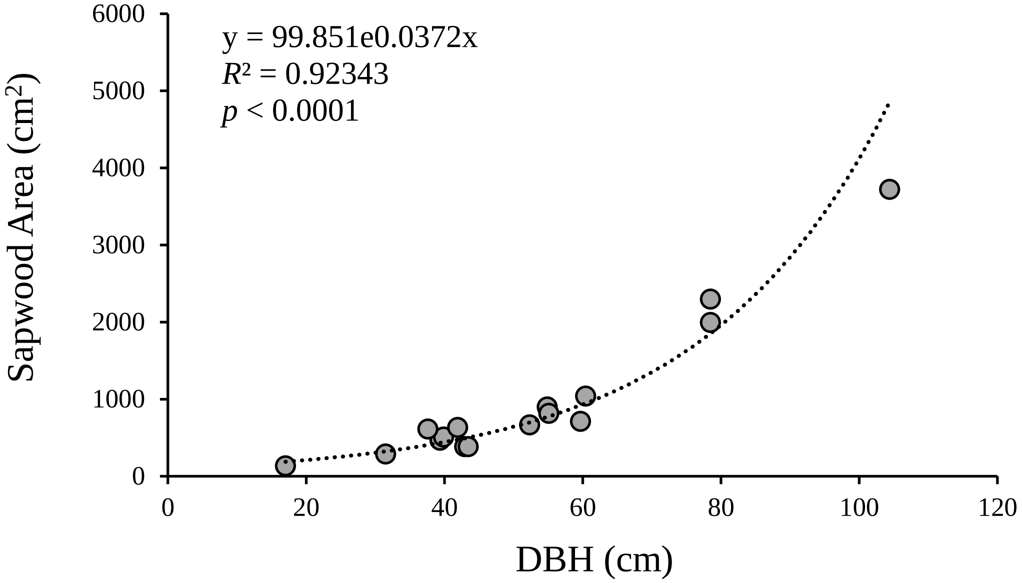

Figure 4. Diameter at breast height (DBH) versus sapwood area for sampled Douglas fir trees at two sites in Humboldt County, California, USA.

Soil Moisture and Creek Discharge

Soil moisture varied seasonally at both sites (Figures 5 and 6, Tables 2 and 3). At the dry site, soil moisture increased with the first major precipitation events in the fall of 2015, where precipitation totaled 5 cm between October 2nd and November 2nd compared to only 1.5 cm in the previous month. At the wet site, despite similar precipitation trends, there was a distinct delay between the onset of rains and increasing soil moisture (Figure 6). Compared to the dry site, mean soil moisture at the wet site was higher throughout the entire sampling period (summer 2015 through summer 2016) and had less of a decline between winter peak (32%) to summer low (13%), a total decrease of about 58% over

248 days. The dry site declined from a peak mean soil moisture content of 26% to a low of 5%, a total decrease of about 80% over 309 days.

Mill Creek (wet site) and Maple Creek (dry site) stream discharge measurements indicate a steady decrease in flow in both streams between late June and late September 2016 (Figures 7 and 8). However, the results for Mill Creek may have been affected by outside influences other than precipitation events such as water withdrawn by private parties. Water may have been withdrawn during the first three sample days, June 17th and 24th and July 1st, and then stopped before the fourth sample day on July 8th. This would explain the rise in flow on July 8th with no precipitation events having taken place, as well as the following steady decline that is attributable to natural summer flow regime.

Table 2. Percentages of soil moisture gathered from samples taken by hand at 15 cm depth at three elevations at the dry site located in Maple Creek, California.

Date	**Upper Plot #5**	**Mid Plot #9**	**Lower Plot #14**	**Mean**
7/22/2015	7	8	11	8
9/2/2015	4	6	6	5
10/2/2015	13	5	13	10
11/2/2015	27	20	29	25
11/17/2015	26	24	28	26
12/4/2015	14	33	17	21
1/4/2016	20	16	23	20
2/4/2016	14	17	16	16
4/7/2016	16	18	15	17
4/30/2016	15	18	19	17
5/11/2016	14	15	15	15
6/18/2016	11	13	13	12
7/10/2016	10	12	-	11
8/4/2016	6	7	6	7
8/25/2016	2	10	5	6
9/21/2016	6	6	4	5
10/5/2016	7	13	9	10
Mean	**13**	**14**	**14**	**14**

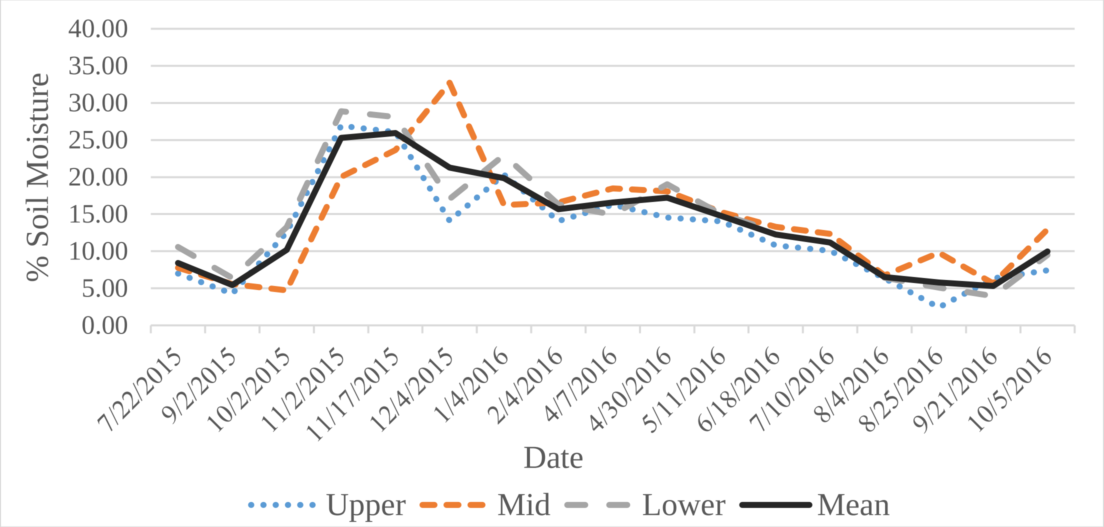

Figure 5. Graph showing the percentages of soil moisture content found in each sample taken at the dry site located in Maple Creek, California, spanning over the sample period lasting from July 22, 2015 through October 5, 2016.

Table 3. Soil moisture data gathered from samples taken by hand at three different elevations at the wet site located in Petrolia, California.

Date	**Upper % Moisture**	**Mid % Moisture**	**Lower % Moisture**	**Mean**
7/10/2015	17	16	17	17
8/10/2015	12	15	13	13
9/5/2015	17	14	13	15
9/26/2015	17	12	16	15
11/8/2015	9	14	19	14
11/30/2015	23	20	24	22
12/10/2015	34	31	31	32
1/23/2016	28	28	35	30
2/19/2016	27	22	28	26
3/4/2016	29	22	25	25
3/27/2016	24	26	23	24
5/1/2016	21	23	21	22
6/10/2016	26	18	22	22
6/17/2016	23	22	21	22
7/7/2016	14	15	15	15
7/22/2016	16	14	17	16
8/14/2016	12	14	14	13
9/27/2016	15	15	15	15
Mean	**21**	**19**	**21**	**20**

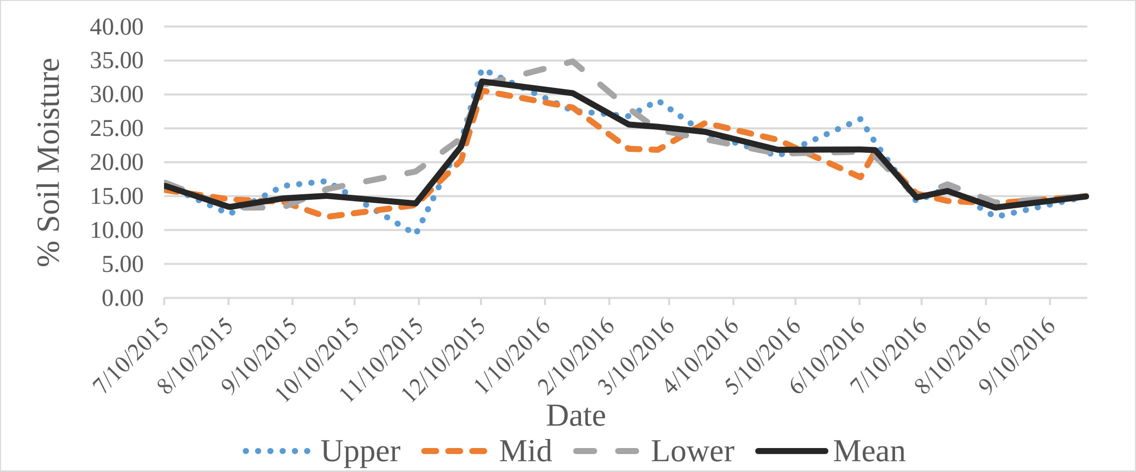

Figure 6. Graph showing the percentages of soil moisture content found in each sample taken at the wet site located in Petrolia, California, spanning over the sample period lasting from July 10, 2015 through September 27, 2016.

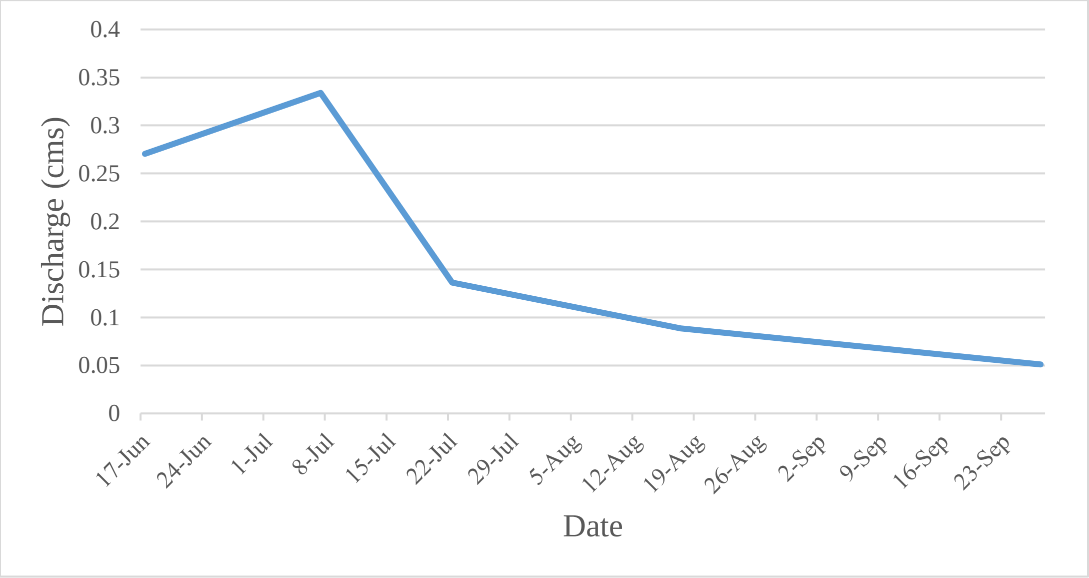

Figure 7. Stream discharge measurements over the summer sample period of 2016 at Mill Creek, California (wetter site).

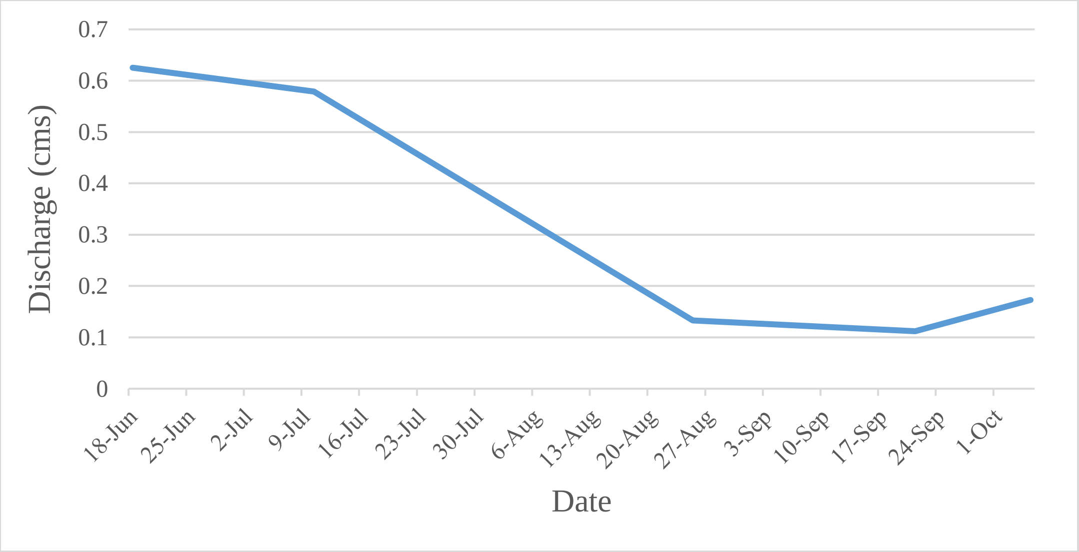

Figure 8. Stream discharge measurements over the summer sample period of 2016 at Maple Creek, California (drier site).

Sap Flow

Weekly Summations

Sap flow decreased throughout the 2015 summer sampling period for all trees at both the wet and dry sites (Figures 9 and 10). Sap flow patterns coincided with those of precipitation, decreasing on precipitation days and then distinctly increasing in the days following. This pattern was more prominent in larger trees. In most cases, the degree to which a tree responded to precipitation events increased with DBH. The duration of increased sap flow following a precipitation event also increased with DBH (Figure 10). There are a few instances where sap flow showed an increase and decrease without a corresponding precipitation event. Precipitation data was collected from local weather stations located at distances of greater than 8 km away from each study site. Therefore, we assume that either rainfall took place at our study site and not at the location of the weather station, as microclimates are prominent in these regions, or there was heavy cloud cover and/or fog that may have caused the sample trees to become less active.

The wet site, with a mean DBH ~10 cm greater than that of the dry, had much more variation in sap flow between trees. Notably, the drop in sap flow over the season was more exaggerated at the dry site and took place at a faster rate compared to the wet site. Compared to summer, spring sap flow was much more variable within each site (Figures 11 and 12), likely due to the greater and more frequent precipitation events during this season. Sap flow increased slightly during spring as solar radiation increased and winter transitioned to summer.

In the drought year of 2015, the steep descent in sap flow begins much earlier (Figure 13) than in the re-watering year of 2016 (Figure 14). This autumnal descent in sap flow occurs at the beginning of August at the dry site and the end of August at the wet site. Exceptionally, in one wet site tree, the largest tree of the study (DBH = 104 cm), summer sap flow increased all the way to the end of August before starting to decrease (Figure 14).

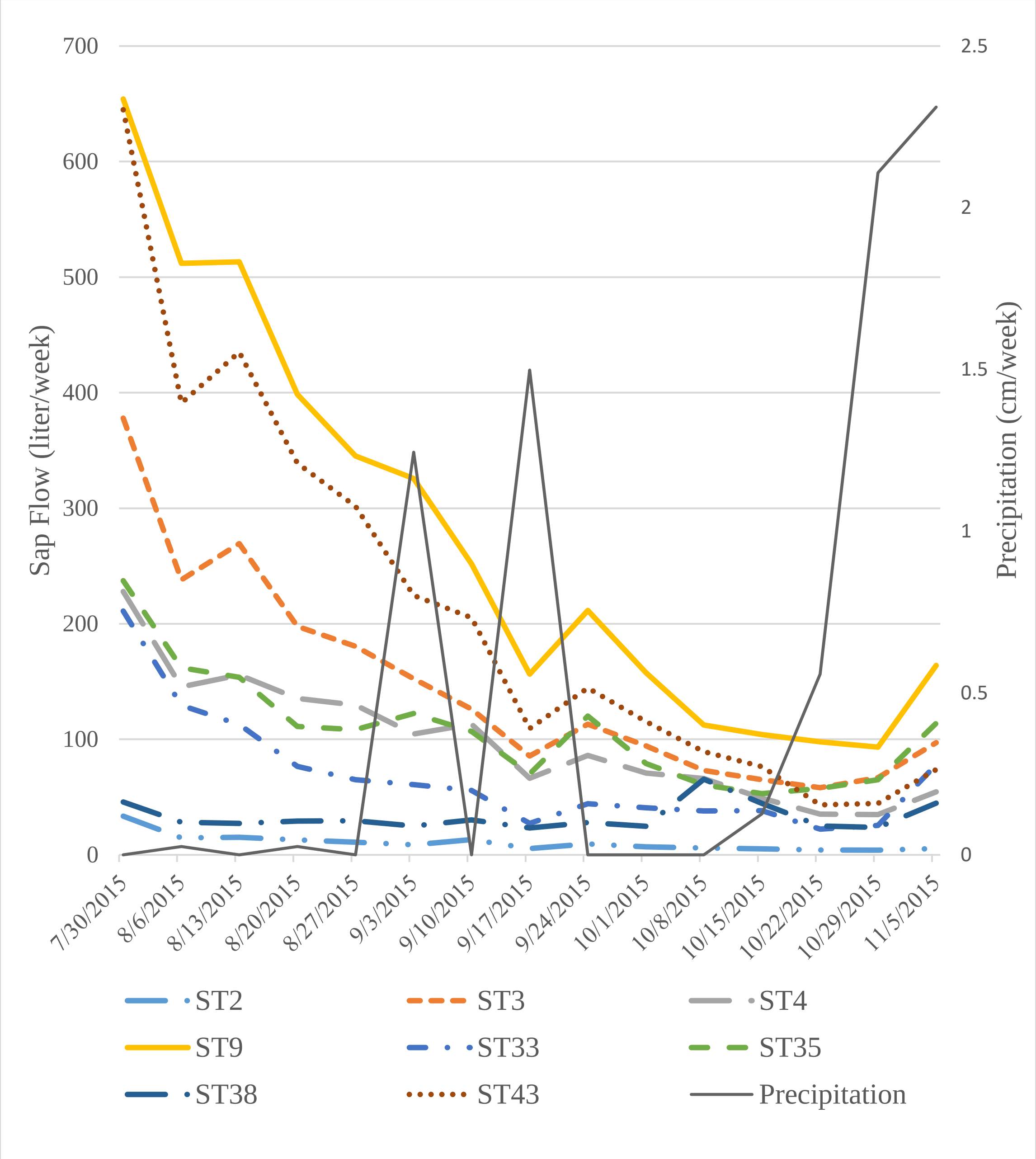

Figure 9. Weekly sap flow summations for all sample trees at the dry site, located in Maple Creek, California, over the summer sample period of 2015, lasting from July 23rd to November 5th.

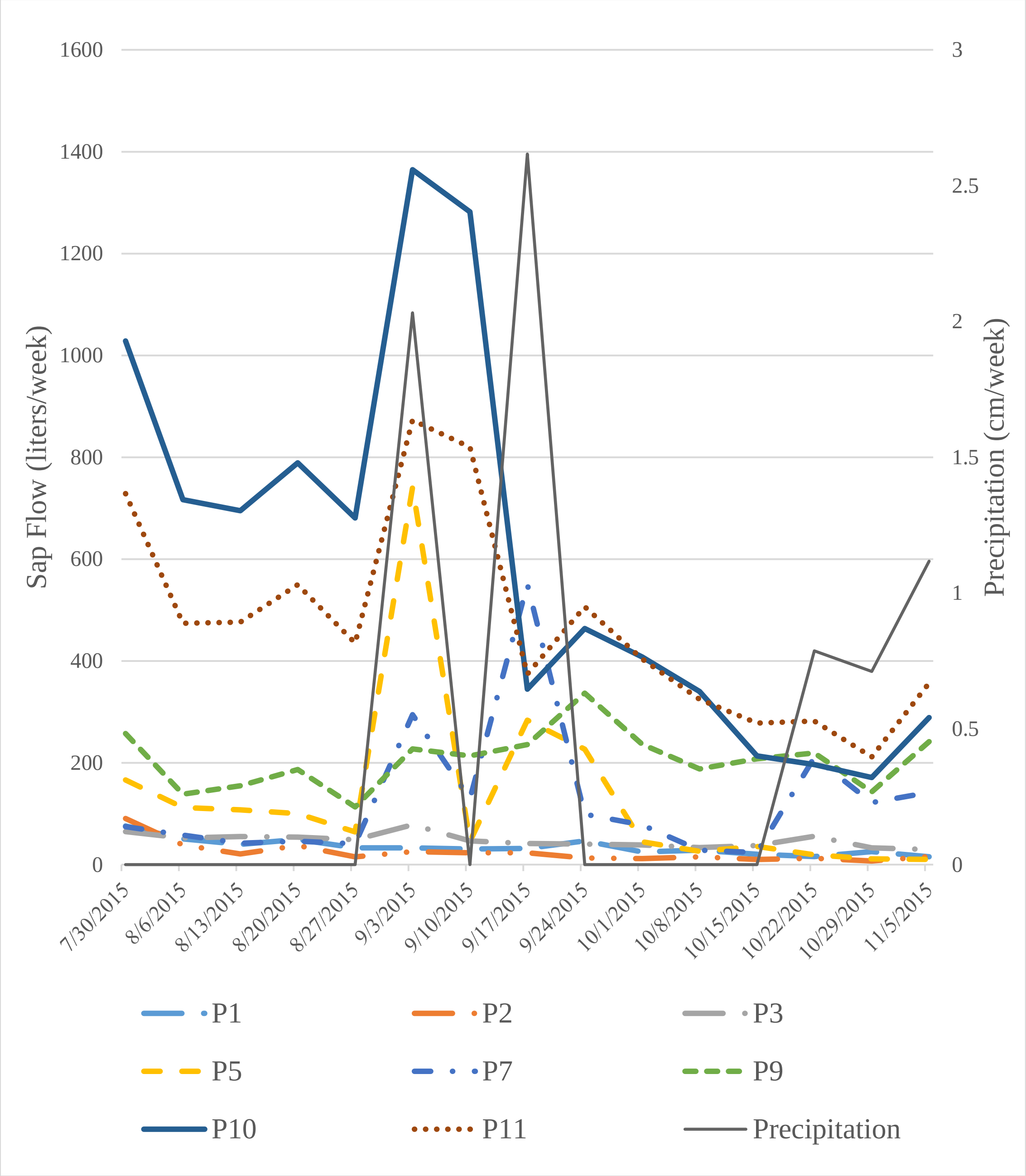

Figure 10. Weekly sap flow summations for all sample trees at the wet site, located in Petrolia, California, over the summer sample period of 2015, lasting from July 23rd to November 5th.

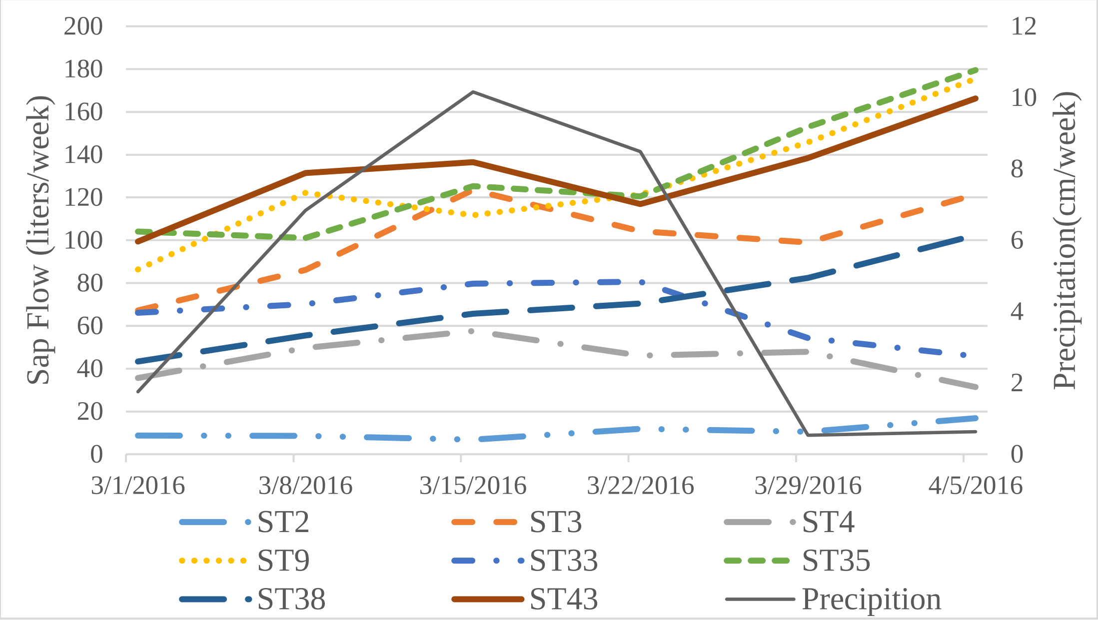

Figure 11. Weekly sap flow summations for all sample trees at the dry site, located in Maple Creek, California, over the spring sample period of 2016, lasting from March 1st to April 5th.

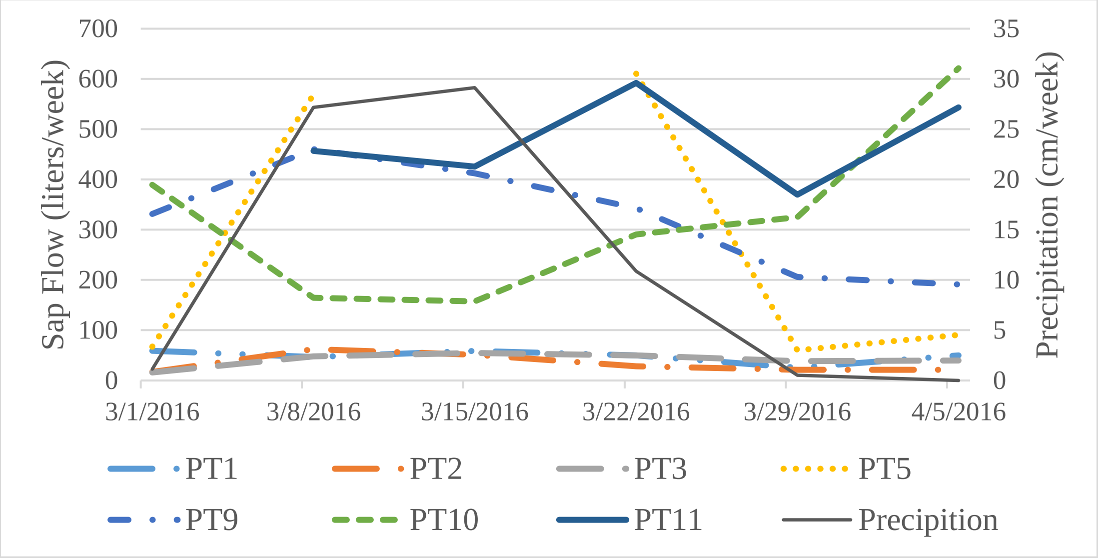

Figure 12. Weekly sap flow summations for all sample trees at the wet site, located in Petrolia, California, over the spring sample period of 2016, lasting from March 1st to April 5th. We are missing data P5 for the week March 8th through March 15th.

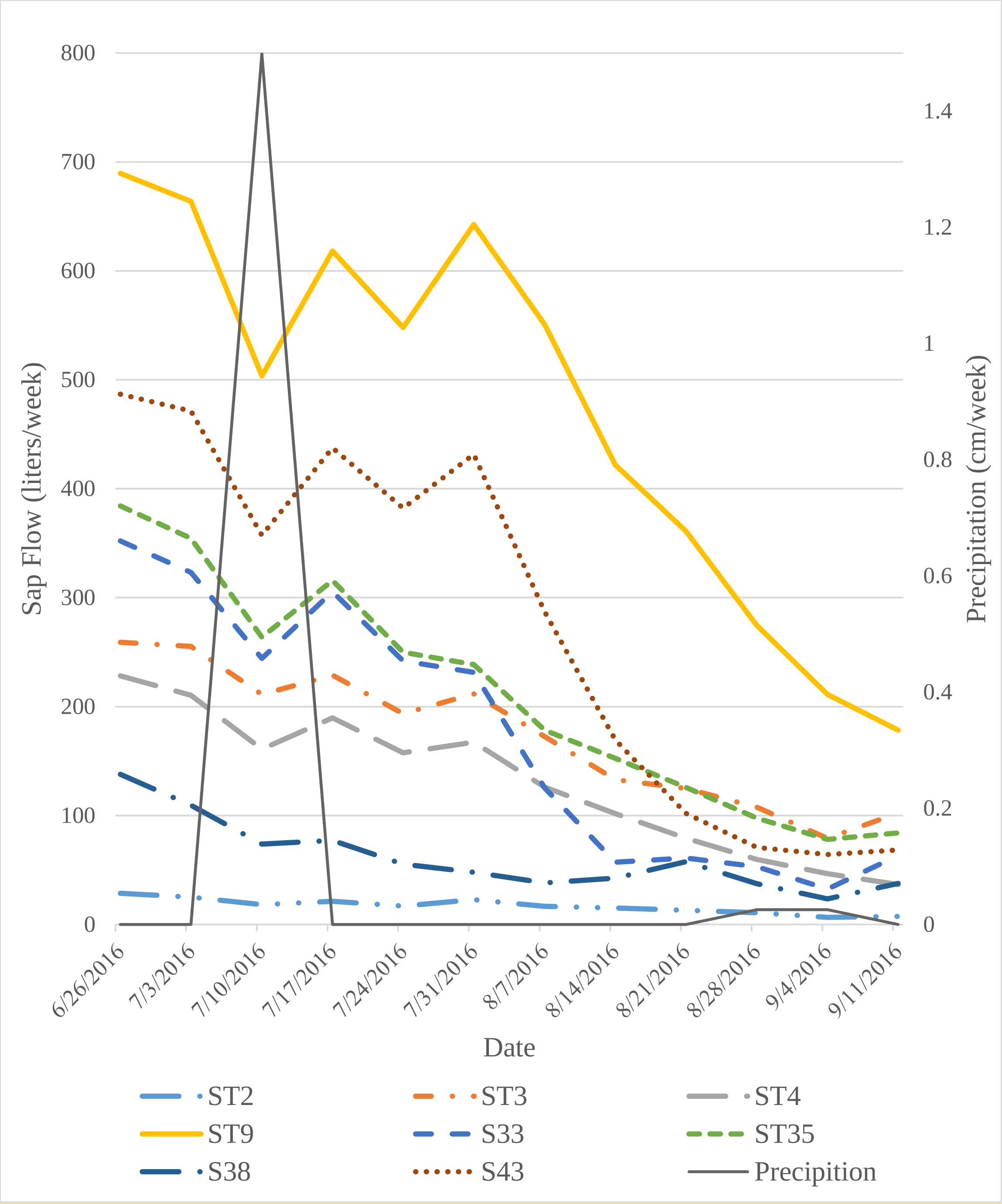

Figure 13. Weekly sap flow summations for all sample trees at the dry site, located in Maple Creek, California, over the summer sample period of 2016, lasting from June 26th to September 11th.

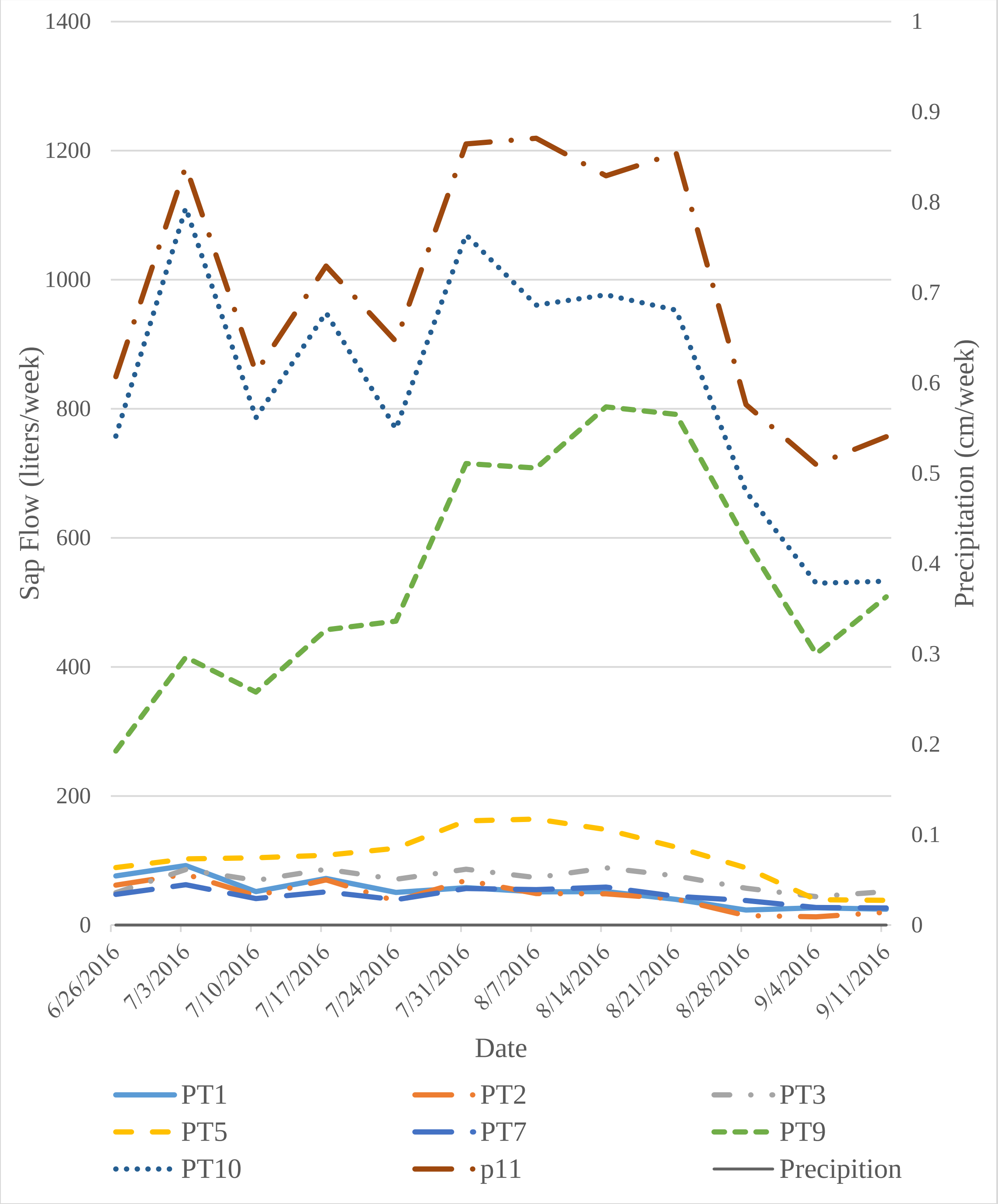

Figure 14. Weekly sap flow summations for all sample trees at the wet site, located in Petrolia, California, over the summer sample period of 2016, lasting from June 26th to September 11th.

Diurnal Pattern and Daily Max

Sap flow rose and fell with a diurnal pattern according to solar radiation levels. Daily maximum sap flow (SF_{max}) declined throughout the growing season (Figures 15 and 16). The decline in sap flow across the growing season was most pronounced at the dry site. For most trees, SF_{max} occurred later in the day as the season progressed. Between the first (July 23rd) and last (September 13th) day of the summer sampling period, the time at which SF_{max} occurred increased at the dry site in 2015 by a mean of about 3 hours and in 2016 by a mean of about 4.6 hours; at the wet site, the time at which SF_{max} occurred increased between the start and end of the summer sampling period in 2015 by a mean of about 4.1 hours and in 2016 by a mean of about 1.6 hours (Table 4). Notably, the smaller trees at both sites experienced the greatest delays in the timing of SF_{max}.

Table 4. Table containing the mean time increase of daily maximum sap flow (SF_{max}) in hours for sample trees at both sites in 2015 and 2016. Sample trees are divided into two categories, large and small, distinguished by having a DBH greater (large) or less than (small) the mean DBH of all the sample trees at that site.

	2015	**2016**
Dry	**3.0**	**4.6**
Small	*4.4*	*7.4*
Large	*1.8*	*1.5*
Wet	**4.1**	**1.6**
Small	*5.8*	*2.8*
Large	*1.3*	*-0.3*

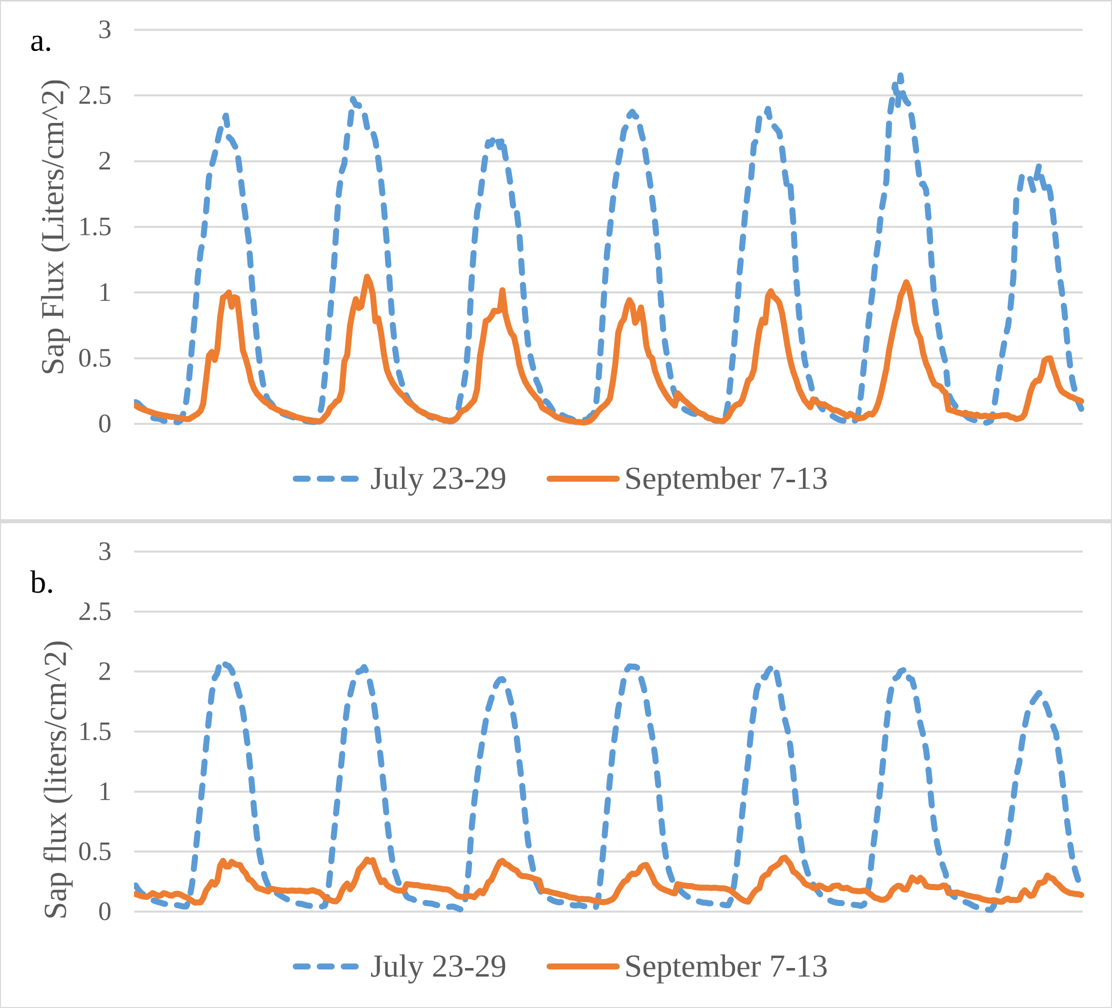

Figure 15. a. Graph showing the first and last week of mean sap flux for the sample trees at the dry site, located in Maple Creek, California, for the summer sample period of 2015. b. Graph showing the first and last week of mean sap flux for the sample trees at the dry site for the summer sample period of 2016.

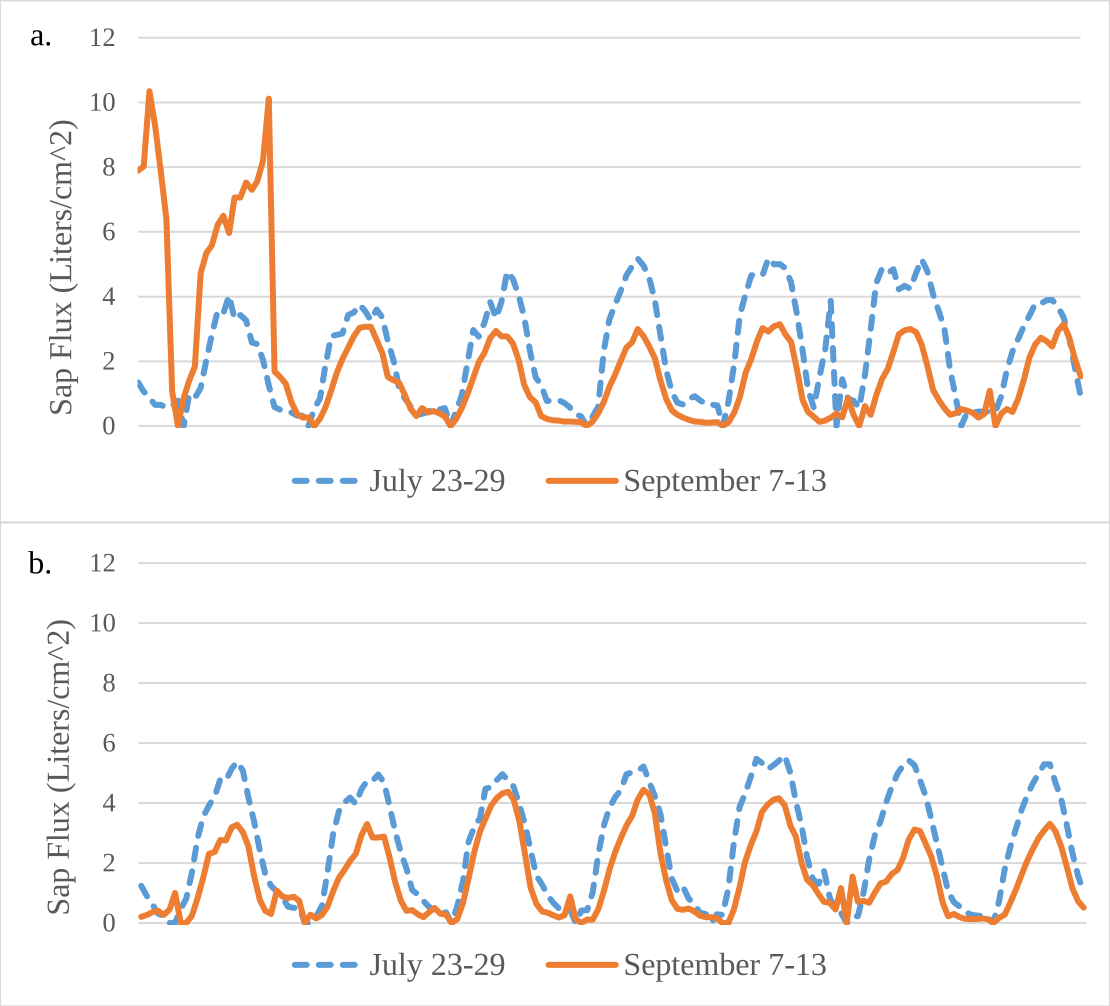

Figure 16. a. Graph showing the first and last week of mean sap flux for the sample trees at the wet site, located in Petrolia, California, for the summer sample period of 2015. The increased sap flow rates for September 7th and 8th are in response to increased precipitation in the week prior. b. Graph showing the first and last week of mean sap flux for the sample trees at the wet site, located in Maple Creek, California, for the summer sample period of 2016.

Inter-Annual and Between Site Trends

To compare water use between years and between sites (Table 5), a common sample period, July 23rd to September 13th, was chosen that overlapped for both sites during 2015 and 2016. Between 2015 (a drought year) and 2016 (a wet year), average total tree water use decreased at the dry site by about 15% and increased at the wet site by about 20%. Remarkably, at the wet site, the largest study tree (DBH = 104 cm) drastically increased water consumption by 240% between 2015 and 2016. We note that at the dry site, the wet year immediately followed thinning treatments, so this reduction in tree water use during the wet year may be due to understory regeneration water use. Between our dry and wet sites, mean daily water consumption (L/day) did not significantly differ in 2015 ($p > 0.05$) or 2016 ($p > 0.05$). At the wet site, DBH was a stronger predictor of water consumption in 2016 ($p < 0.01$) than in 2015 ($p < 0.05$).

During the summer sample period in 2015, mean sap flux density was nearly identical at both sites (~ 0.0127 liters cm^{-2} day^{-1}, Figure 17). However, in the 2016 summer sample period, mean sap flux density was about 20% greater at the wet site (0.0123 liters cm^{-2} day^{-1}) compared to the dry site (0.0098 liters cm^{-2} day^{-1}). In small trees at the wet site, sap flux density was positively correlated with TVI in 2015 (Figure 18, $R^2 = 0.97$, $p = 0.01$) and 2016 ($R^2 = 0.93$, $p = 0.035$). In large trees at the wet site, sap flux density was weakly negatively correlated with TVI in 2015 (Figure 18, $R^2 = 0.32$, $p > 0.05$) and 2016 ($R^2 = 0.65$, $p > 0.05$). No strong correlations between water use and TVI were observed at the dry site.

Table 5. Table containing values for the total sap flow, liters consumed per day, and sap flux density, expressed as liters/cm^2/day, for two summer comparison sample periods in 2015 and 2016, lasting from July 23rd through September 13th, for both sites. The percent change in water consumption from the summer sample period in 2015 to 2016 is listed in the last column.

	Summer 2015:			**Summer 2016:**			
Dry Site:							
Sample Tree	**H2O Consumed Season Total (L)**	**H2O Consumed (L/day)**	**Sap Flux Density (L/cm^2/ day)**	**H2O Consumed Season Total (L)**	**H2O Consumed (L/day)**	**Sap Flux Density (L/cm^2 /day)**	**% Change in H_2O Consumption from '15 to '16**
S2	116.05	2.23	0.0098	100.80	1.94	0.0085	-13.14
S3	1642.20	31.58	0.0134	1015.01	19.52	0.0083	-38.19
S4	1084.33	20.85	0.0144	673.60	12.95	0.0090	-37.88
S9	3183.25	61.22	0.0219	2868.59	55.17	0.0197	-9.88
S33	761.20	14.64	0.0120	713.93	13.73	0.0113	-6.21
S35	1073.60	20.65	0.0087	1046.73	20.13	0.0084	-2.50
S38	233.25	4.49	0.0036	307.56	5.91	0.0047	31.86
S43	2698.78	51.90	0.0181	1327.88	25.54	0.0089	-50.80
mean	**1349.08**	**25.94**	**0.0127**	**1006.76**	**19.36**	**0.0098**	**-15.84**
Wet Site:							
P1	334.89	6.44	0.0083	297.70	5.72	0.0073	-11.11
P2	263.34	5.06	0.0046	275.63	5.30	0.0048	4.67
P3	429.80	8.27	0.0060	514.16	9.89	0.0072	19.63
P5	1381.53	26.57	0.0179	814.20	15.66	0.0106	-41.06
P7	708.35	13.62	0.0063	327.23	6.29	0.0029	-53.80
P9	1425.12	27.41	0.0032	4840.89	93.09	0.0109	239.68
P10	5421.65	104.26	0.0216	6127.40	117.83	0.0244	13.02
P11	8532.24	164.08	0.0339	7633.97	146.81	0.0303	-10.53
mean	**2312.11**	**44.46**	**0.0127**	**2603.90**	**50.07**	**0.0123**	**20.06**
2-Site Mean	**1830.60**	**35.20**	**0.0127**	**1805.33**	**34.72**	**0.0111**	**2.11**

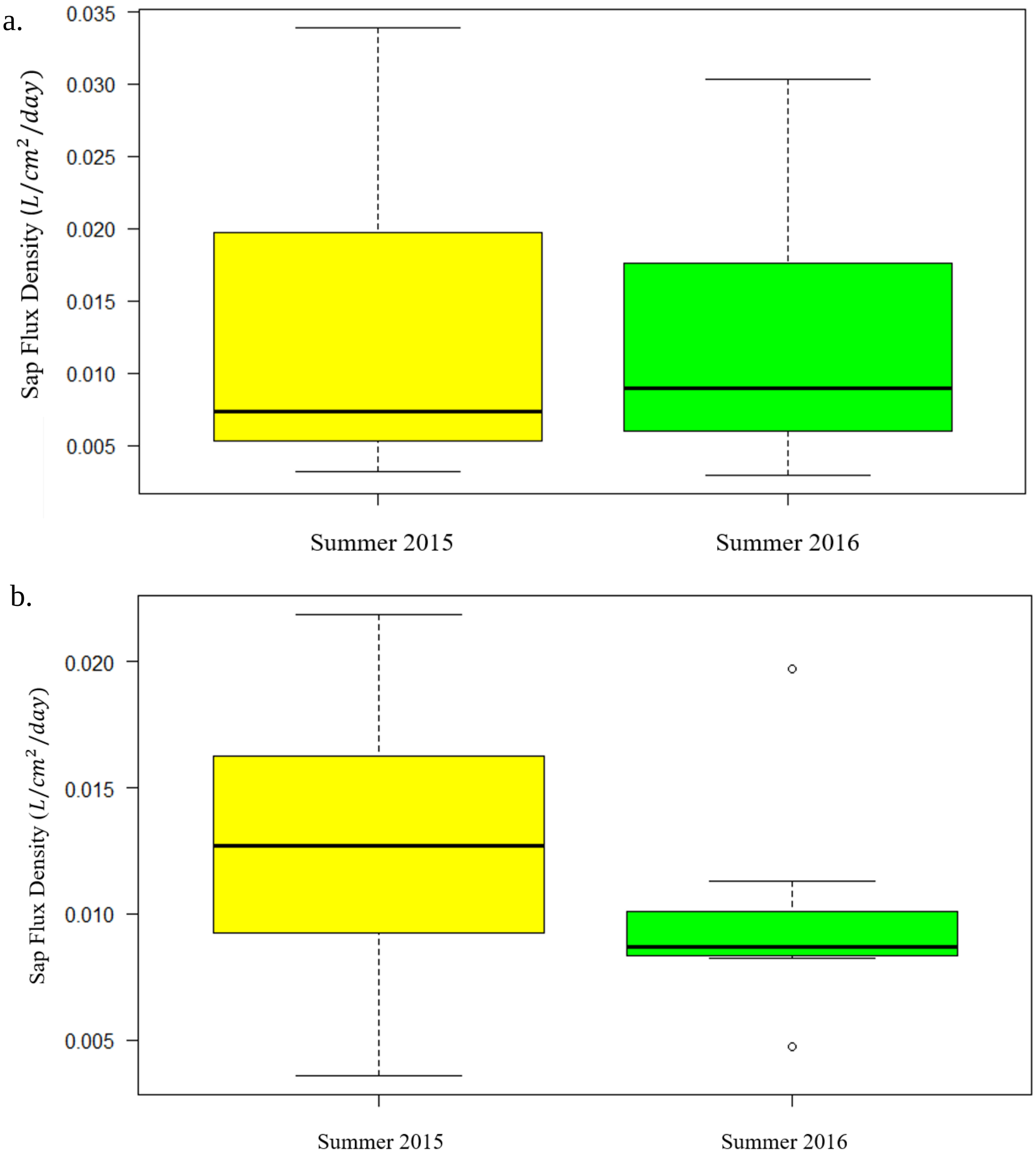

Figure 17. a. Boxplots of sap flux density in liters/cm^2/day for both summer sample periods for sample trees at the dry site located in Maple Creek, California.
b. Boxplots of sap flux density in liters/cm^2/day for both summer sample periods for sample trees at the wet site located in Petrolia, California.

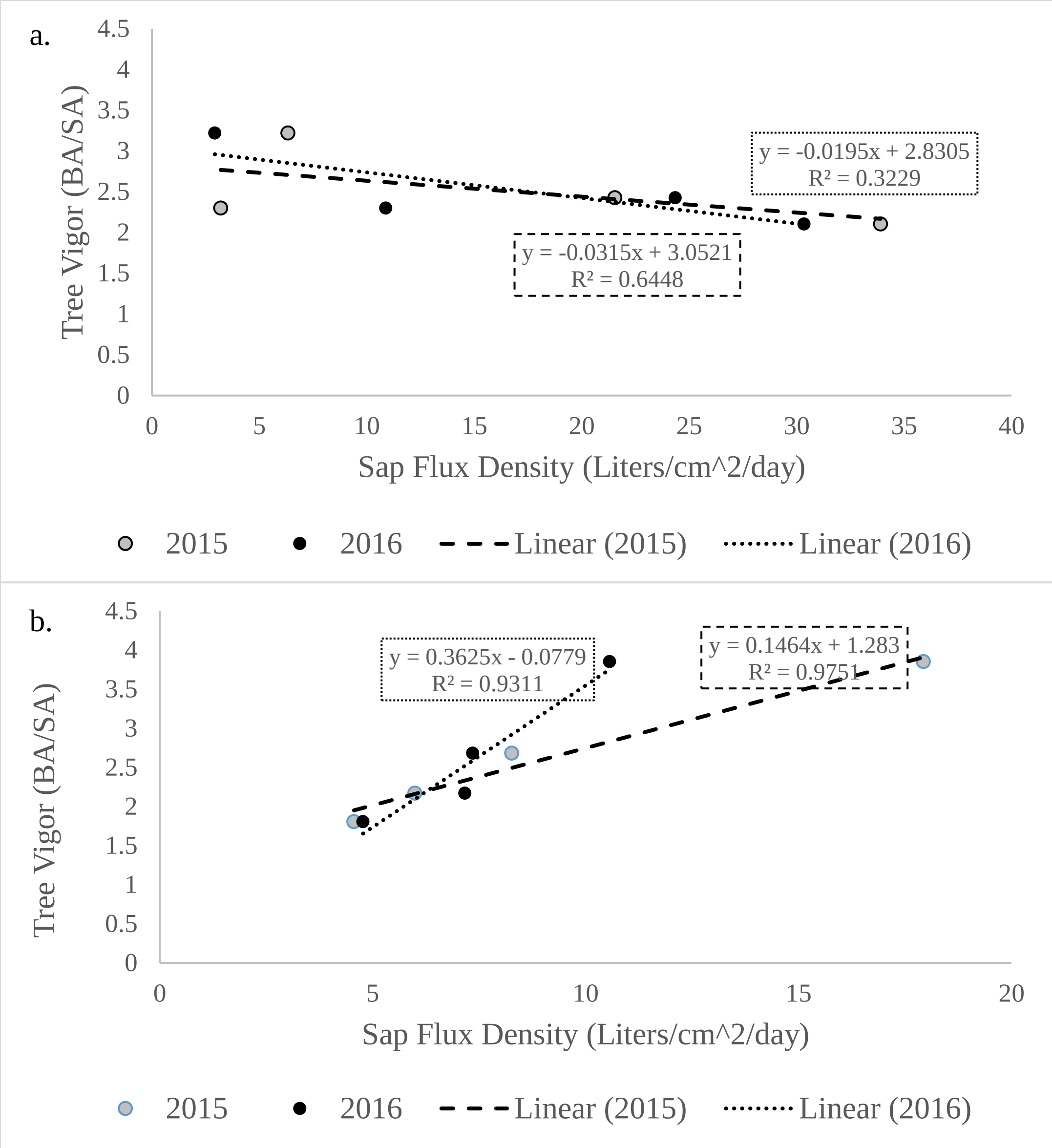

Figure 18. a. Linear model showing relationship between Sap Flux Density and Tree Vigor for small sample trees at the wet site, located in Petrolia, California. b. Linear model showing relationship between Sap Flux Density and Tree Vigor for large sample trees also at the wet site.

Nighttime Water Use

Nocturnal sap flow, defined as sap flow taking place between sunset and sunrise (sunset and sunrise times were adjusted for latitude and day of year), followed an inverse pattern to total sap flow for the same sample periods. Unlike total sap flow, nighttime sap flow increased throughout both summers as water availability decreased (Table 6). The percent of nighttime sap flow was determined as the percent of sap flow occurring between sunset and sunrise out of the total sap flow for a given 24-hour day. Mean nighttime water use varied greatly between sites and between years (Figures 19 and 20). In 2015, a higher percent (35%) of water was consumed during the night at the wet site compared to at the dry site (22%). The opposite was true for 2016, when the dry site used a higher mean percent of nighttime water (33%) compared to the wet site (22%). The change in percent nighttime water use from 2015 to 2016 was significantly different between the two sites ($p < 0.05$). On average, trees at the wet site used 36% less nighttime water in 2016 compared to 2015, while trees at the dry site used 33% percent more nighttime water in 2016 compared to 2015. There was no significant correlation at either site between tree size and percent nighttime water consumption, although a few trees showed distinctly different trends. One small tree (DBH = 40 cm) at the dry site consumed more than 50% of its water at night during both summers. At the wet site, the largest tree (DBH = 104 cm) consumed almost 70% less nighttime water in 2016 than in 2015, which was more than twice the difference of most other trees at this site.

Table 6. The percent of the total water consumed during nighttime hours in 2015 and 2016 for each sample tree, as well as the rate of change from 2015 to 2016, represented as a positive or negative percent change.

	Sample Tree	**% of Water Use Occuring at Night '15**	**% of Water Use Occuring at Night '16**	**% Change in Nighttime Use**
Dry Site:	S2	29	34	14
	S33	30	47	57
	S38	58	57	-2

	Sample Tree	% of Water Use Occuring at Night '15	% of Water Use Occuring at Night '16	% Change in Nighttime Use
	S4	11	18	59
	S3	13	37	183
	S35	22	31	43
	S9	16	16	-2
	S43	14	25	78
Mean:		**22**	**33**	**33**
Wet Site:	P1	15	20	29
	P2	35	27	-24
	P3	35	22	-39
	P5	34	29	-4
	P7	34	27	-20
	P9	50	16	-69
	P10	16	16	-2
	P11	20	23	14
Mean:		**35**	**22**	**-36**
2-Site Mean:		**27**	**28**	**3**

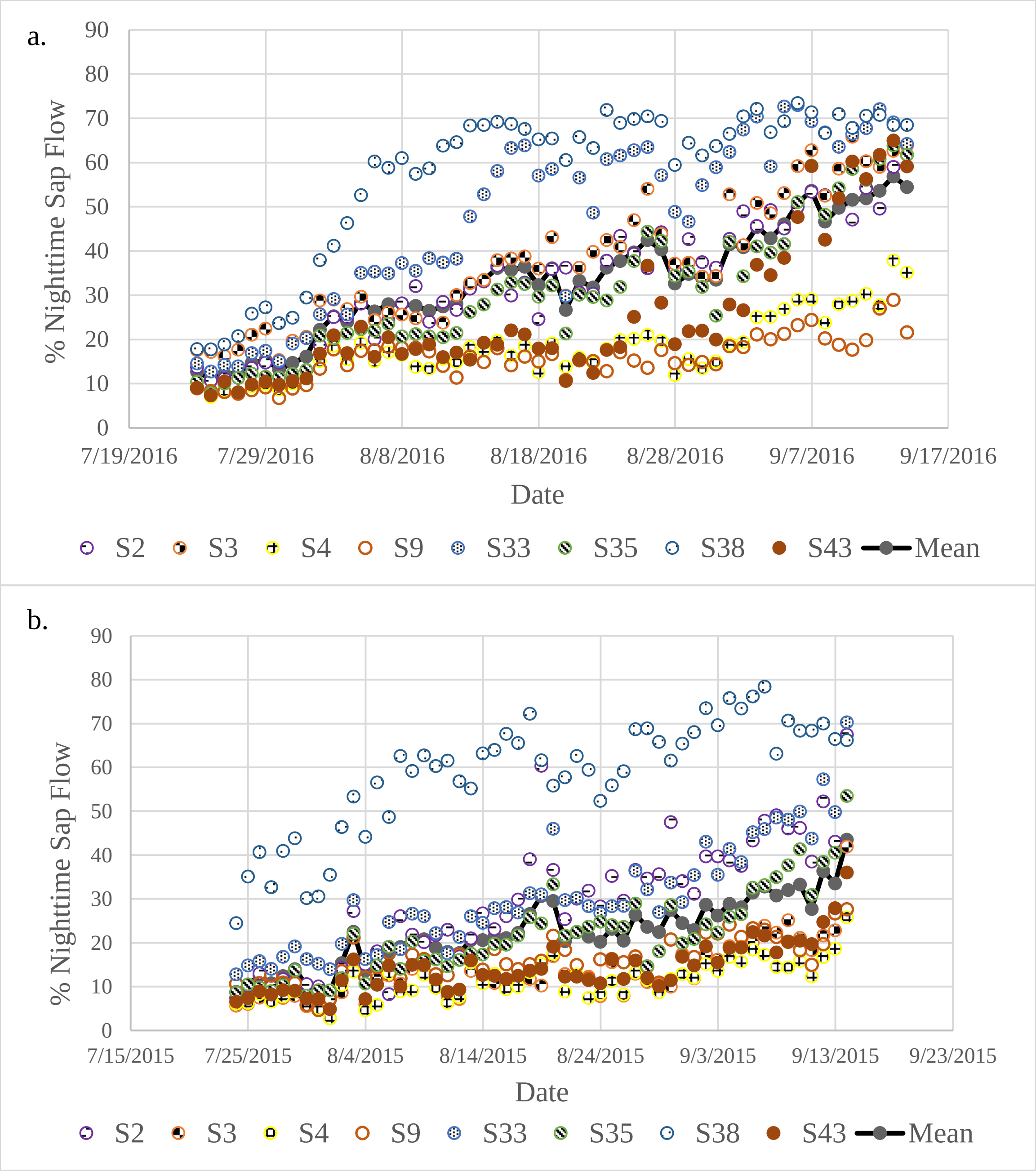

Figure 19. Percentage of sap flow occurring during nighttime at the dry site, located in Maple Creek, California, during the summer sample period of a. 2015 and b. 2016.

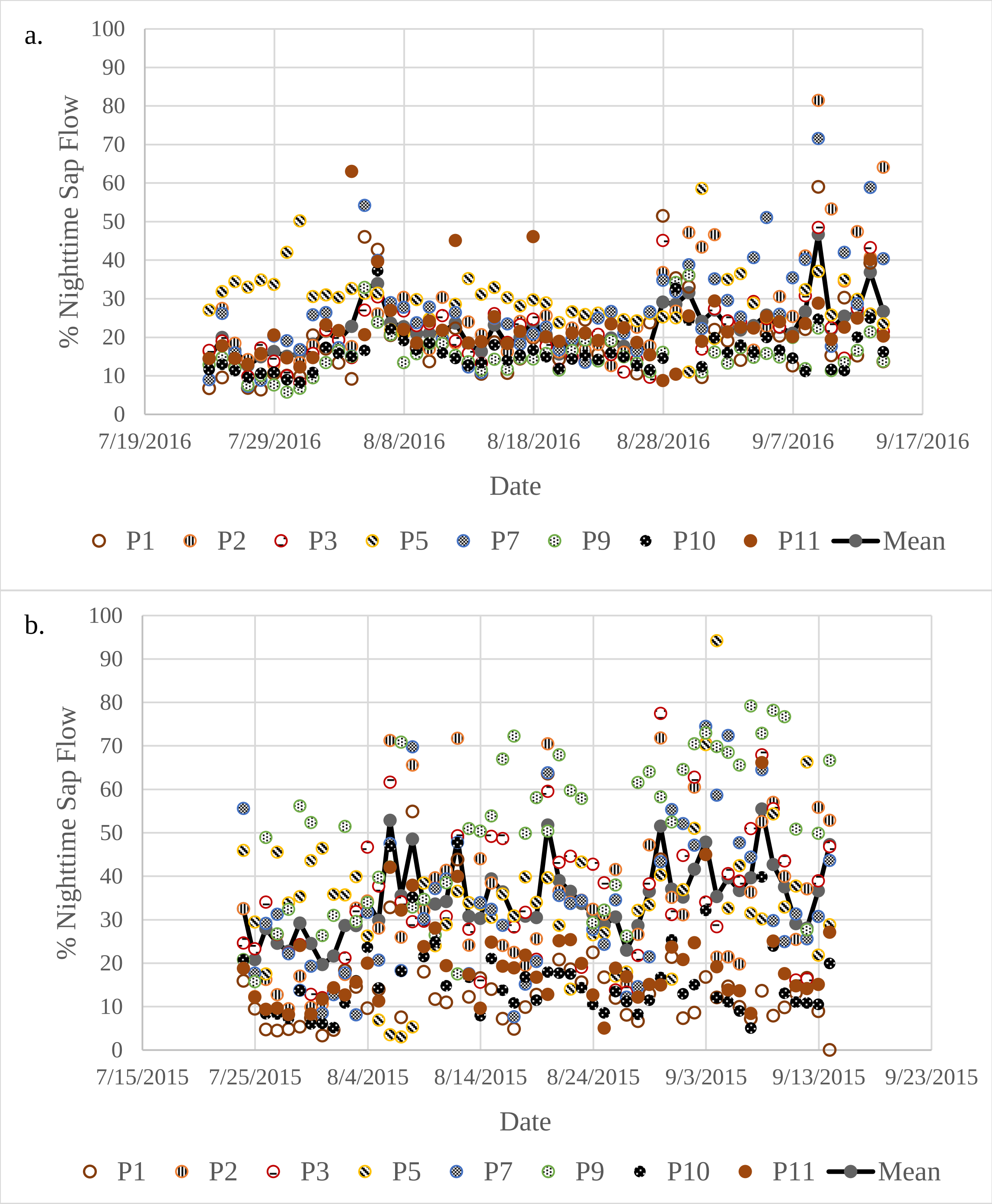

Figure 20. Percentage of sap flow occurring during nighttime at the wet site, located in Petrolia, California, during the summer sample period of a. 2015 and b. 2016.

Local Density, VDR Plots, and Water Consumption

Local Density

Local tree density was nearly three times greater at the wet site compared to at the dry site (Table 7). At both sites, local density was an insignificant factor in explaining sap flow and sap flux density in 2015 and 2016 summer sample periods ($p > 0.05$). This lack of a significant relationship between water consumption and local density may be the artifact of a limited sample size. Thus, this relationship warrants further investigation with a larger sample.

Table 7. Values for local density, defined as cm^2 of Douglas-fir basal area at breast height within 6 meters of the corresponding sample tree.

Sample Tree	**Local Density (cm^2)**
Dry Site:	
S2	1642
S33	10956
S38	1051
S4	6458
S3	0
S35	0
S9	910
S43	7394
Mean	**3551**
Wet Site:	
P1	602
P2	8476
P3	15834
P5	8938
P7	15608
P9&10	4030
P11&12	13860
P13&14	4838
Mean	**9023**
2-Site Mean	**6287**

Variable Density Treatments

At the dry site, although water use was not significantly correlated to VDR or coniferous cover (defined as the amount of basal area within each VDR plot) in the 2015 or 2016 summer sampling periods, VDR and coniferous cover were significantly related to the change in water use from 2015 to 2016. Trees in high basal area reduction treatments had significantly higher water use in 2016 than in 2015 (Table 8, $p < 0.05$). Density retention level was positively correlated with the magnitude of change in tree water consumption between the 2015 and 2016 summer sampling periods (Figure 21, $R^2 = 0.66$, $p = .01$). We also found a strong relationship between the inter-annual change in water use and post-treatment conifer cover (Figure 21, $R^2 = 0.82$, $p = 0.002$).

Table 8. Table listing each sample tree at the dry site with corresponding thinning treatments and pre and post coniferous stand composition.

Sample Tree	**DBH (cm)**	**VDR (%)**	**Pre-Conifer (%)**	**Post-Conifer (%)**
S2	17.0	45	74	33
S3	54.9	30	42	13
S4	42.9	30	42	13
S9	59.7	30	94	28
S33	39.4	100	58	58
S35	55.1	0	41	0
S38	39.9	100	58	58
S43	60.5	15	36	5
Mean	**46.2**		**55**	**26**

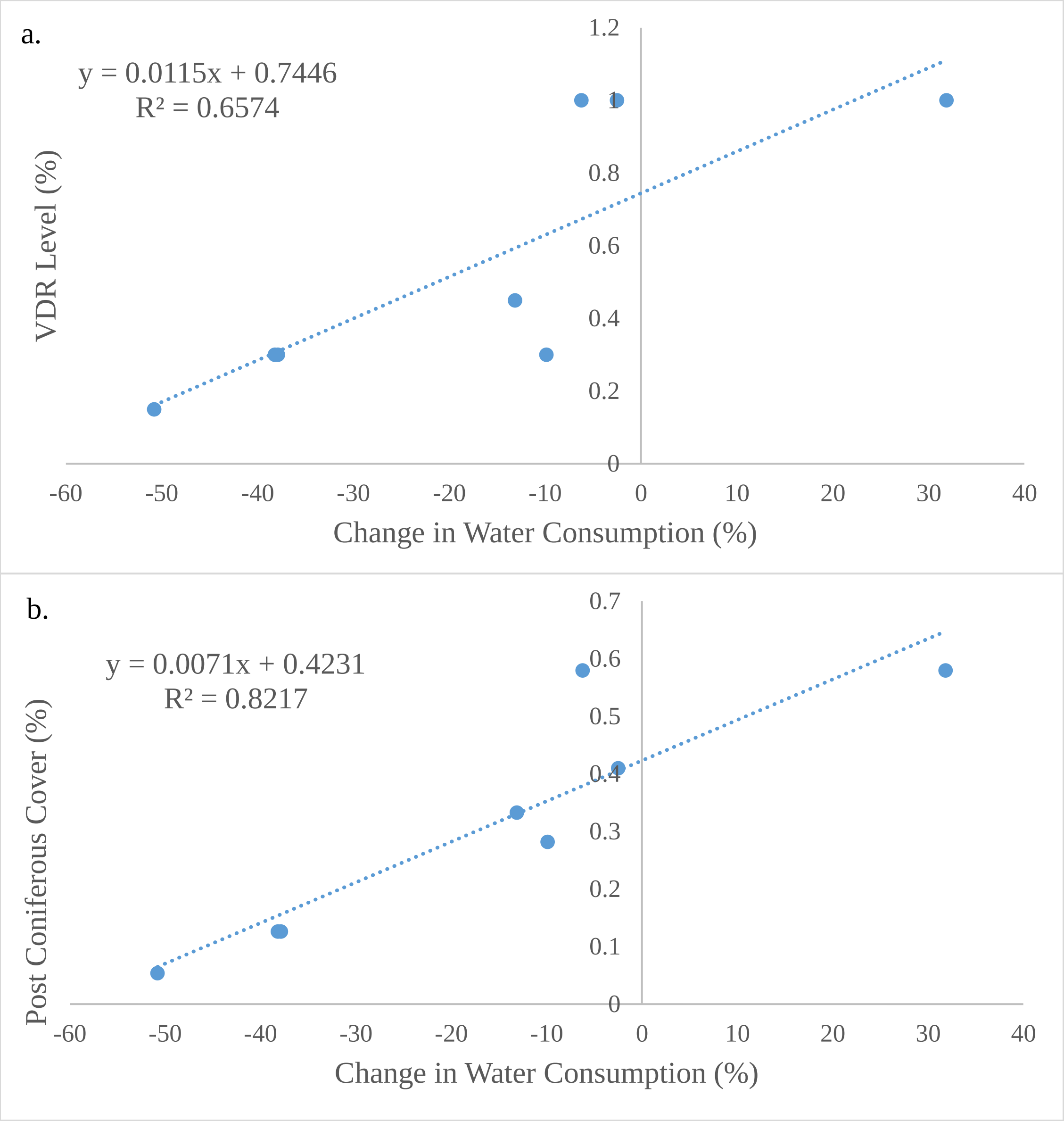

Figure 21. a. Linear relationship between the levels of density retention applied in thinning treatments and the change in water consumption from 2015 to 2016 at the dry site. b. Linear relationship between the percent of coniferous cover post treatment and the change in water consumption from 2015 to 2016 at the dry site.

DISCUSSION

General Water-use Trends

Mean diurnal sap flow peak decreased over both summer sample periods at both sites. These decreases are correlated with similar decreases in soil moisture levels and stream discharge in their associated watersheds. The rate of decrease was more prominent during the most water limiting sample periods (occurring in 2016 at the dry site and 2015 at the wet site). Sap flow velocity values were within a reasonable range and seem credible when compared to other studies (Link et al., 2014). The wet site, having undergone thinning treatments in 2009, displayed the expected response to a drought year followed by a rewatering year, with mean water consumption increasing by about 20% from 2015 to 2016. At the recently thinned (fall 2014) dry site however, sap flow decreased by almost 16% between the drought year and the rewatering year. This pattern starkly contrasts the expected typical positive correlation between sap flow and precipitation. At this recently treated site, increased understory and regeneration growth in the wake of thinning treatments and in response to a post-drought re-watering period likely decreased tree water availability, thereby explaining the observed decrease in sap flow between 2015 and 2016 (McDowell et al. 2008). In 2016, DBH was a good predictor of water use for sample trees at the wet site, while DBH was a far worse indicator in 2015 when the trees were still experiencing stress from long-term drought.

DBH was not a good predictor for either years for sample trees at the dry site, where we assume there was increased water stress during both years, as stated above.

Signs of Water Stress

Nighttime Water Use

Our late summer sap flow measurements from the fourth year of a 1,000-year drought (Asner et al., 2016) coupled with measurements from the following re-watering year highlight poorly understood tree responses to extreme water stress. For example, our findings show that nighttime sap flow contributes significantly (11-58%) to total sap flow at both sites. While previous studies that have reported substantial (up to 25%) amounts of nighttime sap flow in Douglas-fir trees (Phillips et al., 2003, Cermak et al., 2006), none have demonstrated such high percentages as found here. Our findings are within a believable range, as nighttime sap flow percentages up to 70% have been reported in pines (Klein 2016).

Nighttime transpiration may occur due to a coupling of incompletely closed stomata and high vapor pressure deficit (Fisher, 2007), defined as the difference between the amount of water vapor pressure the air can hold and how much it is actually holding. However, both study sites are influenced by fog and therefore not likely to have high overnight vapor pressure deficit. Alternatively, it is possible that the observed overnight water flux reflects a refilling period where stored water within the tree bole fills cavitated xylem conduits. Cavitation occurs as a result of low water availability (McDowell et al., 2008). Consequently, the observed increase in nighttime water use could reflect the refilling of increasing xylem cavitation as the historical summer drought progressed. This positive correlation between nighttime sap flow and water stress is further supported by the observation that mean percent nighttime sap flow was higher during summer sample periods of lowest water availability, as quantified by the lowest mean tree water consumption (2015 at the wet site due to the fourth year of drought and 2016 at the dry site due to post-thinning effects).

Delayed Timing of Peak Sap Flow

Another factor suggesting the presence of cavitation and re-filling is the delayed timing of daily peak sap flow throughout both summer sample periods, a phenomenon known as hysteresis where sap flow response to solar radiation is delayed due to depleted stem water storage (O’Grady et al., 1998). In low stress environments where water is non-limiting, sap flow directly responds to solar radiation levels and, incidentally, photosynthetic rates. However, when water is limiting but solar radiation is high, tree transpiration and cavitation refilling draw on water stored predominantly in the lower portion of the bole (Domec and Gartner 2001). In extreme drought circumstances, water storage supplementation is inadequate, and as a result, a decoupling occurs between solar radiation and bole sap flow (Klein 2016): although transpiration may have slowed or stopped in the leaves, breast height sap flow measurements do not reflect this (as exemplified in this study). Instead, due to xylem conduit refilling, sap flow responds to cavitation frequency, thereby delaying peak sap flow relative to peak transpiration rate. As drought severity increases throughout summer, transpiration increasingly relies on internally stored water rather than soil water. Our observed delay in peak sap flow timing between the beginning and end of the sample period was about 1.6 hours in the lower stress summer and up to 4.6 hours in the higher stress summer. This increased delay in the more stressful summer could be due to prolonged sap flow as bole-stored water was used to refill cavitated xylem conduits.

Cavitation and Relationship to Tree Size

Old growth Douglas-fir trees are more vulnerable to cavitation than younger trees, and older sapwood lower in the bole is more vulnerable than younger sapwood near treetops (Phillips et al., 2003, Cermak et al., 2006, Domec and Gartner, 2001). Due to this greater vulnerability and subsequent refilling of cavitated conduits, mean nighttime sap flow for large Douglas-fir trees can be about 20% of total sap flow, while in small trees it is typically only about 10% (Domec and Gartner, 2001). Thus, our finding of nighttime sap flow constituting a mean of 22% of total sap flow during the re-watering year seems within the known range for this species.

However, in our study mean nighttime sap flow was generally higher in smaller trees than in larger trees. In our smallest tree (DBH = 17 cm), nighttime sap flow accounted for 32% of total sap flow during both summers. In contrast to this finding, other studies have observed lower nighttime sap flow percentages in small trees compared to larger trees (Domec and Gartner, 2001) and relatively low (10%) and consistent nighttime sap flow percentages during drought (Phillips et al., 2003). We speculate that our observed high nighttime water use at the dry site likely reflects increased stress related to increased post-thinning competition, but there may be other factors influencing high nighttime water use in small trees at the wet site, and possibly at the dry site as well. Our largest tree (DBH = 104 cm) consumed about 50% of its total water use at night in 2015 but less than 16% of its total water use in 2016. A similar shift in nighttime consumption as a response to and release from drought by the larger trees was also observed in the Phillips et al. study (2003).

Old-Growth Adaptive Response to Water Stress

Observations of our largest study tree, a likely remnant of the pre-logging old-growth forest structure, indicate an alteration of typical water use patterns to overcome drought-related stress. Compared to smaller trees, taller, old-growth trees are more susceptible to cavitation due to increased gravitational tension on the water column (Woodruff et al. 2007, Phillips et al. 2003) and likely to have greater water storage capacity. The water stored may have diminished water potential, and thus be more easily transported upwards (Domec and Gartner, 2001). Despite this implied occurrence of cavitation and compensation, we also found that the largest tree consumed nearly 2.4 times more water during the re-watering year than it did during the previous drought year. This increased water consumption during the first post-drought year suggests that the observed low water consumption during drought was due to stomatal closure to minimize water loss under dry conditions. Thus, the ability to reduce sap flow and use bole-stored water (reflected as nighttime sap flow) during drought appears to confer in large trees a notable resilience against unfavorable conditions.

Predicting Water Use in Periods of Low Water Availability

Our results suggest that drought-related stress increases variability in Douglas-fir water use patterns. In 2016, DBH was a good predictor of water use for sample trees at the wet site, while DBH was a far worse indicator in 2015 when the trees were still experiencing stress from long-term drought. DBH was not a good predictor for either years for sample trees at the dry site, where we assume there was increased water stress during both years, attributed to drought during 2015 and increased competition from applied treatments during 2016. There was no correlation found between local density and water use. Although, this may be due to the small sample size in this study, and thus requires further investigation to be ruled out as an important factor in water-use response to drought. When under stress, it appears that factors other than size may play an important role in determining water consumption for small trees, most notably access to solar radiation.

Water Use in Relation to Spatial Distribution

There was no correlation found between local density and water use, however, spatial distribution in relation solar radiation did appear to have an impact on water use. At the wet site, trees with the highest levels of sap flux density in 2015 are located within the southern portion of the stand near a bordering meadow (Figure 3), and, therefore, were likely exposed to greater solar radiation than other trees at this site. While larger sample trees that had higher water use also had the advantage of height, the smaller sample trees showing high water use during the drought year did not, clarifying the importance of their spatial distribution. When under stress, it appears that factors other than size may play an important role in determining water consumption for small trees, most notably access to solar radiation. Typical stand water-balance models do not consider spatial distribution, which may result in an underestimation of tree water use (Kostner et al. 1998), particularly when concerning drought constraints.

Drought Response to Thinning Treatments

Following thinning, reduced competition due to basal area removal and canopy opening strongly influences stand water use. Our findings suggest that competition has a stronger influence on water use than soil water availability: dry site trees consumed ~16% more water during the fourth consecutive drought year than during the rewatering, year when there was high competition from the regenerating understory. As sap flow measurements were not taken prior to the 2014 thinning treatments, we assume that the observed higher water use in 2015 is a direct response to treatment. This assumption is supported by past studies that found a spike in conifer stand water consumption directly following treatment (Morikawa et al., 1986). Post-treatment increases in water consumption are attributed to greater solar radiation and water availability due to initially reduced competition. However, our observed rapid decrease in tree water use in the second post-treatment year contrasts with other studies that report initial increases in water use lasting at least three years before stand water use returns to pre-treatment levels (Aussenac et al., 1988).

One possible explanation for this rapid decrease in tree water use following thinning could be the timing of treatments relative to the drought and rewatering years. During a post-drought rewatering year, vegetative growth can be greater than normal (Horst and Nelson, 1979, Fekedulegn et al., 2003). In this scenario, the abnormally productive period then corresponds to the second year post treatment of 2016, where it was combined with increased solar radiation from the opening of the canopy layer, ultimately resulting in a truncated period of increased stand-level sap flow as a result of increased competition for water resources from regeneration and understory growth. This conclusion is further backed by the strong positive correlation ($R^2 = 0.82$) between post-treatment conifer cover and the change in water consumption between 2015 and 2016 summers. In areas retaining greater conifer cover, trees consumed more water than trees in areas with high conifer removal, indicating that a factor related to conifer removal decreased tree water consumption between 2015 and 2016.

Conclusions

Our findings provide building blocks for future evaluations of water use by PNW coniferous forests. We demonstrate the importance of spatial distribution relative to solar radiation in determining water consumption in small trees (DBH < 104 cm) and ultimately could provide a more accurate evaluation of water balance predictions during future drought periods when paired with existing methods (DBH, height, relative extractable soil water, leaf area index). We also show that large trees appear to have a great capacity for resilience by decreasing water consumption during periods of severe drought, thereby potentially increasing water availability to smaller trees (Van Mantgem and Stephenson, 2007). Nighttime sap flow levels in this study exceeded those previously published for Douglas-fir, highlighting the immense impact of water stress on stand water use patterns and the intriguing potential for nighttime sap flow as a tool to gauge stand resilience. Due to our small sample size, further research is needed to confirm these findings and further assess stand and individual water use in relation to stand and local density. When under stress from low water availability, the amount and timing of Douglas-fir water consumption diverges from normal patterns such that further study will be needed to accurately predict forest responses to increased temperatures projected in the Pacific Northwest.

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