Effects of artificial, stand-level induced drought and thinning on *Pseudotsuga menziesii* plantation eco-physiology, and soil respiration

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Abstract

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Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is an important tree species in the Pacific Northwest (PNW), ranging from central British Columbia to Mexico. Douglas-fir is widely used for wood production and silvicultural applications such as thinning, and fertilization have led to increases in productivity. Climate change in the PNW is predicted to increase temperatures, and less precipitation in the summer is expected to increase drought effects and reduce Douglas-fir plantation growth and productivity. Therefore, better understanding the impacts of climate change on Douglas-fir growth and physiology, the interactive effects of silviculture and reduced water availability (i.e., drought) on Douglas-fir plantations in PNW is needed. This study was conducted at UW's Pack Forest to evaluate the effects of thinning and drought stress on tree physiology and growth. Throughfall exclusion panels were used to create an artificial drought on the study site, reducing 40 % of throughfall precipitation. The first and second studies examined the effects of thinning and drought stress on tree physiological responses, and stem growth. Tree physiological traits such as sapflow density, photosynthesis, leaf water potential and stem growth increased with thinning and decreased with drought. Thinning increased physiological measures and stem growth, and drought stress reduced physiological measures and stem growth. The physiological responses and stem growth on the combination plot (thinning and throughfall exclusion) were similar to the control plot, which indicated that thinning mitigated the drought effects on tree physiology and growth. The third study examined the impacts of thinning and drought on soil respiration. Soil respiration decreased on the throughfall exclusion plot, but soil respiration on the thinned plot was similar to the control plot. Q_{10} which is the temperature sensitivity of soil respiration, is also negatively affected by the two treatments. Drought treatment lowered the soil respiration by decreasing soil moisture which directly affected root production and breakdown of the organic matter forming the substrate for heterotrophic respiration. Thinning initially reduced soil respiration due to a reduction in tree root respiration, then the soil respiration reached a similar level as the control, likely due to decomposition of dead roots. Overall results indicate that thinning can be beneficial in Douglas-fir plantations experiencing drought stress by increasing soil water availability and serve as a mitigating tool to climate change.

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CHAPTER 1

Introduction

Climate change is probably the most threatening issue global-wide in the 21st century. One of the most significant effects of climate change is increasing temperature as a consequence of human activity and industrialization in the 20th century. Climate change is expected to increase air temperature by 1.8 to 4.0 °C and mean precipitation by 7 % during the 21st century (IPCC 2007). Van Vuuren et al. (2008), indicate the average global temperature could increase from 0.8 to 2.6 °C by the year 2050 and 1.4 to 5.8 °C by the year 2100, respectively. Increased temperature will bring more frequent drought, of severe intensity and longer duration, and be the major reason for changes in the hydrologic cycle (Sheffield and Wood 2008). Furthermore, this climate warming can have significant potential effects on temperature and precipitation of forest ecosystems, leading to problems of productivity, nutrient cycling, and water resources. Consequently, increasing temperature will generate increasing water deficit, accelerating lower productivity, and higher mortality because of drought and fire (Raymond and McKenzie 2012). Also, the increased temperature may alter carbon allocation to roots and shoots, tree growth rate, and canopy closure in forests.

The Pacific Northwest (PNW) is likely to experience this climate change with models predicting that annual mean temperature will increase ranging from 0.5 to 2.6 °C and 1.5 to 3.2 °C in 2020 and 2040 respectively (Mote et al. 2003; Randall et al. 2007; Mote and Salathe 2010). The PNW is also predicted to have more precipitation in winter seasons than at present. However, warmer and drier summers are predicted, increasing drought stress on forest ecosystems and species. Warmer and drier summers are likely to decrease the quantity and duration of snowpack, decrease summer runoff, increase summer temperature, and therefore increase forest water deficits (Mote et al. 2003; Randall et al. 2007; Mote and Salathe 2010).

Drought can become the most critical stress for plant physiology (Shao et al. 2009). Water is an essential factor influencing plant physiology, such as transpiration, and photosynthesis because water plays crucial roles in physiological processes and occupies 80-90 % of fresh weight in herbaceous plants and more than 50 % of fresh weight of woody plants (Kramer and Boyer 1995; Lambers et al. 1998). In response to drought stress, stomatal closure occurs to limit water loss from the leaves, and this regulates CO_2 movements from outside to inside leaves. As a result of stomatal closure, the reduction of intercellular CO_2 concentration occurs which is the main cause of reducing photosynthesis (Farquhar and Sharkey 1982). Decreases in water-related mechanisms such as sapflow density and leaf water potential also occur (Pangle et al. 2012; Samuelson et al. 2014; Zhang et al. 2016). Drought also lowered leaf litterfall, flowering, and foliage production, and delayed the timing of flowering (Limousin et al. 2012). Long-lasting drought (both intensive and/or moderate) can result in decreases in tree growth, biomass accumulation, and tree mortality (Orwig and Abrams 1997; Koch et al. 2004; Liu et al. 2018; Gavinet et al. 2019).

Silvicultural treatments such as initial spacing and species composition, thinning, and fertilization are usually applied to increase wood production, and growth in diameter and height, to reduce within-stand competition, and nutrients, and to accelerate carbon assimilation. Even and adequate initial spacing has positive effects on tree diameter and height growth, and crown developments; diameter and height increased with increase in initial spacing and crown length, and width also increased in wider spacing treatment plots (Curtis and Reukema 1970; Harrington and Reukema 1983; Hein et al. 2008). Thinning results in an increase of soil moisture availability and reduction of plant water stress in remaining trees because it reduces stand transpiration and rainfall interception losses (White et al. 2009). Also, light availability increases with thinning, since thinning changes canopy architecture (Goudiaby et al. 2011). Therefore, thinning has a positive effect on dense forest stands by reducing water stress and light competition. It is generally believed that decreased density by thinning reduces stand-level transpiration while individual tree level transpiration may increase (Breda et al. 1995). Density reduction also affects positively on light and nutrient availability (Blanco et al. 2005). Forest growth is often limited by nitrogen availability especially in temperate forests (LeBauer and Treseder 2008). Fertilization has been applied to increase biomass increment and tree growth. Not only increases in stem wood but also leaf area index (LAI) and light interception in Douglas-fir forest were found where nitrogen (N) fertilizer was applied long term along the Interior Northwest and Pacific Northwest (Balster and Marshall 2000; Brooks and Mitchell 2011). It is recognized that N fertilizer accelerates net photosynthesis and increases tree growth (Gebauer and Schulze 1991).

A few studies have attempted to demonstrate that silvicultural applications could reduce or mitigate the drought impacts on tree growth, tree physiology, and tree mortality (Ward et al. 2015; Will et al. 2015; Wightman et al. 2016; Gavinet et al. 2019). These previous studies were conducted in the field using “throughfall exclusion” which manipulates rainfall to create an artificially induced-drought so that the effects of silvicultural applications on drought impacts can be evaluated. However, these throughfall exclusion (TFE) studies were established mostly in drought-prone areas and/or tropical rain forests. In mesic areas such as the PNW, TFE studies have not been conducted prior to this research. As climate change scenarios indicate that the PNW is expected to experience more frequent and severe drought in the future, this study is needed to predict the effects of drought on this area and the impacts of silvicultural application as a mitigation tool to lessen the impact of drought. We established the throughfall exclusion and thinning

treatments on a mesic productive Douglas-fir plantation at the UW's Pack Forest, WA to evaluate the effects of thinning and drought on tree physiology, stem growth, and soil respiration, and the potential mitigation effect of thinning against drought impacts. Thinning enhanced physiological traits such as sapflow density, water potential, and photosynthesis as well as stem growth and basal area increment. However, drought reduced those physiological traits and stem growth while basal area increment was not affected. Thinning increased soil moisture but soil respiration remained unaffected. Drought reduced soil respiration, soil moisture and soil respiration sensitivity to temperature (Q_{10}).

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CHAPTER 2

Effects of artificial, stand-level induced drought and thinning on *Pseudotsuga menziesii* plantation eco-physiology and water recovery

Abstract

Summer drought is expected to increase with climatic change in the Pacific Northwestern United States in the 21st Century. We used a stand-level field experiment to understand drought impacts on Douglas-fir, and the potential of lowering competition through thinning to mitigate drought stress. The site environment (temperature, precipitation, soil moisture, and relative humidity), sapflow density and growth were monitored for 5 years. Throughfall exclusion panels created an artificial drought (ambient vs. 40 % reduction) and thinning overstocked stands reduced water stress in Douglas-fir plantations (35-40 year-old). Throughfall exclusion had little effect on temperature, relative humidity, and vapor pressure deficit but decreased soil moisture and water potential; the thinning treatment increased temperature and relative humidity. Thinning increased the sapflow density, predawn, and midday leaf water potential, photosynthesis, stem increment, and days of stem expansion.

In contrast, drought-induction with throughfall exclusion decreased sapflow density, midday leaf water potential, photosynthesis, and stem increment. Sapflow density was 20% higher on thinned plots and 28 % lower on throughfall exclusion plot on average than that on control plot over three years. The throughfall exclusion panels were removed at year 3, and soil water and sapflow density increased after removal, confirming the experimental induction of drought stress.

The lowest sapflow densities were observed in the 2015 and 2017 drought years, and summer months generally showed lower sapflow density at the end of the experiment in 2018 than at the beginning, regardless of treatment, demonstrating the persistence of the drought of 2015-2017. The thinning treatment served as an effective drought mitigation technique, with the thinned but drought-induced stand, having higher photosynthesis, sapflow density, and growth than the control sites. If climate change increases drought frequency and intensity, reduced plantation stocking on production sites may be sufficient to prevent growth losses and/or widespread mortality.

Keywords: throughfall exclusion, thinning, drought stress, sapflow density, *Pseudotsuga menziesii*, water recovery

Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is a widely distributed tree species, ranging from central British Columbia to Mexico, and occupies a range of climates from maritime (i.e., moderate winter temperature with ample precipitation) along the Pacific Coast to continental climates with cold winters and dry summers in the Rocky Mountains (Zhang and Hebda 2004; Watts et al. 2015). Douglas-fir is the region’s most common commercial forestry species and is grown in pure plantations representing 77% of the saw timber and 87% of sales in Washington and Oregon states in 2005 (Howard 2007). Ecologically, Douglas-fir is an important component of naturally regenerated forests including old-growth forests in the Pacific Northwest (PNW) (Waring and Franklin 1979) and stores over 50% of aboveground carbon in Oregon state (Donnegan et al. 2008).

The Pacific Northwest (PNW) is predicted to warm, with increased summer drought frequency and potentially more winter precipitation under numerous climate change scenarios. Models simulating climate change in the PNW suggest that annual mean temperature will increase between 0.5-2.6 °C and 1.5-3.2 °C in 2020 and 2040 respectively (Mote et al. 2003; Randall et al. 2007; Mote and Salathe 2010). Warmer and drier summers are likely to decrease quantity and duration of snowpack, decrease summer runoff, increase summer temperature, and therefore increase forest water deficits (Mote 2003; Mote et al. 2003; Randall et al. 2007; Mote and Salathe 2010). While warmer temperatures could initially increase forest productivity (especially on the coast where Douglas-fir is energy limited—Albright and Peterson 2013), continued increasing temperature could increase water deficits, decrease net productivity and increase mortality due to drought, fire, and pests (Chmura et al. 2011; Raymond and McKenzie 2012). Littell et al. (2008) indicate the growth of Douglas-fir is limited more by water availability than temperature and solar radiation, and an increase in growing season temperature without an increase in summer precipitation may result in decreased growth. Dominant tree species such as Douglas-fir and western hemlock in the PNW may be affected by severe drought (Rehfeldt et al. 2006; Coops and Waring 2011), and some models predict major contraction in the range of Douglas-fir (Littell et al. 2010).

Douglas-fir response to water stress and/or water deficit typically show: reductions in photosynthesis and stomatal conductance and a decrease in predawn water potential and reduced rate of transpiration, and reductions of chlorophyll fluorescence (expressed as: Fv/Fm) in Douglas-fir seedlings (Unterscheutz et al. 1974; Brix 1979; Fang-yuan and Guy 2004; Warren et al. 2004; Aghai et al. 2019). While seedlings are more easily measured, there is uncertainty as to how well seedling studies predict mature tree responses; mature trees have better-developed root systems which should increase their ability to moderate the effects of drought.

Investigating drought stress in the field, especially at large scale, is challenging because it is hard to alter and regulate the environmental conditions, interactions between weather events and edaphic conditions, and the occurrences of severe, rare drought events (Fay et al. 2000). Therefore, measuring physiological mechanisms of mature trees in native forest systems has been limited. Experimental designs manipulating precipitation at the stand scale have used permanent and movable rain-out shelters, subcanopy/understory panels and gutters, and above canopy irrigation systems to alter the amount and timing of precipitation reaching the soil (Svejcar et al. 1999; Fay et al. 2000; Nepstad et al. 2002; Beier et al. 2004; English et al. 2005; Wullschleger and Hanson 2006). In forested areas with mature trees, through-fall exclusion (TFE) methods at large-scale have been applied in efforts to experimentally generate drought at the tree, stand, and ecosystem levels (Nepstad et al. 2002; Wullschleger and Hanson 2006; Fisher et al. 2007; da Costa et al. 2010). TFE structures have been used in rain forests in Amazon, Brazil, and Mediterranean forests (Nepstad et al. 2002; Limousin et al. 2009; Misson et al. 2010; Misson et al. 2011; Rodríguez-Calcerrada et al. 2013). However, only a few studies have been conducted over multiple years (Hanson et al. 2001; Ogaya and Peñuelas 2007; da Costa et al. 2010), limiting inferences on long-term impacts of drought. Previous field experiments have focused on unmanaged forests, and/or young stands, less than 10 years.

Thinning can increase drought resistance by decreasing stand transpiration, rainfall interception losses, and changes in canopy architecture (Goudiaby et al. 2011; Gebhardt et al. 2014). Thinning also reduces within–stand water competition and root competition, improving water use status (Sucoff and Hong 1974; Bréda et al. 1995; Misson et al. 2003; Moreno and Cubera

2008), and increases soil moisture and light availability (Mayor and Rodà 1993; Bréda et al. 1995; Blanco et al. 2005). As a consequence, trees remaining after thinning have increased net photosynthesis due to reductions in light, water, and nutrient competition (Moreno-Gutiérrez et al. 2011; Giuggiola et al. 2016). Thinning enhances basal area increment of remaining trees, and even under drought conditions, sustained tree growth in thinned stands is observed (McDowell et al. 2003; Kohler et al. 2010).

In the PNW, Douglas-fir production system thinning regimes have received considerable attention (Bose et al. 2018), with commercial thinning guidelines based on stand density metrics (e.g., Curtis Relative Density; Curtis 1982). Thinning increases diameter growth (Worthington 1966) and basal area increment (Roberts and Harrington 2008). Chase et al. (2016) found that thinning enhanced basal area growth of Douglas-fir, and pre-commercial thinning could reduce effects of environmental stress.

In this study, we induced drought in a maturing (rotation-aged) Douglas-fir plantation to understand the effects of climate change projected increased drought stress on managed forests on a mesic productive site in western Washington. We used throughfall exclusion panels equipped with gutters to remove ~ 40 % of throughfall precipitation. The effects of thinning were incorporated into the field design to assess the potential for typical thinning to reduce drought stress. Field instrumentation documented soil moisture, temperature, relative humidity, sapflow density and growth over 5 years. The approach allowed us to test the effects of 1) artificially induced-drought and thinning on the physical environment, and 2) Douglas-fir physiological responses to the field treatments including sapflow density, photosynthesis, water potential, and stem growth.

Materials and Methods

Site description

The study was carried out in a Douglas-fir plantation (studied trees age 35-40 years-old) at 535-565 m, located (lat. 46°49’18.20”N, long 122°17’33.71”W) in the University of Washington’s Experimental Pack Forest, just outside of Eatonville, WA (Figure 1). Pack Forest has maritime climate, with annual average of maximum of and minimum temperatures 15.6 °C and 5.8 °C respectively, and 900-1400 mm annual precipitation. Monthly average precipitation is 100 mm with the driest months in July and August. Summer drought is common June - September with precipitation often less than 60 mm/month and periods of weeks without measurable precipitation are common (Gessel et al. 1990). Precipitation and temperature range from 900 mm to 1,400 mm and - 8.2 °C to 35 °C with an average of 10.1 °C, respectively on the study site from an on-site weather station. The site has a south aspect on a gently sloping ridge 0 to 20 %. Douglas-fir with western hemlock (*Tsuga heterophylla* (Raf.) Sarg) were planted with 1,250 trees per ha (TPH) on the site in 1979, and pre-commercially thinned (PCT) to 470 TPH in 1993. The PCT removed western hemlock, creating pure Douglas-fir plantations. The parent material of soil is a Vitrandic Haploxeralf of the Wilkeson Series (Gravelly silt loam). The depth of soil to bedrock is ~1-2 m.

Experimental Design

The study was designed as a 2 x 2 factorial with two levels of precipitation; Control and an approximate 40 % reduction with panels excluding throughfall (i.e., TFE treatment;Figure 2), and two levels of thinning treatment (TH); none and 25 % basal area reduction (from Curtis RD > 56, down to ~ 40). After thinning, stand density (SD) and basal area (BA) in the TH plot were reduced by 34 % and 25 %, respectively, and reductions of SD and BA in the THTFE were lowered 32 % and 26 %, respectively (Table 1). The thinning treatment was conducted February-March 2014, with cables to minimize skidding disturbance, and slash was removed from all plots and piled away from sites. Four 0.16 ha plots were created (Figure 2), with 0.06 ha interior trees instrumented. Two un-thinned plots had an average of 79 trees in 0.16 ha with 28 trees on average in 0.06 core plots, and two thinned plots were reduced to an average of 46 trees from the starting stocking of 67 trees. The 0.06 ha core plots had 25 trees and 13 trees pre- and post-thinning respectively (Figure 3). Site panels and gutters were installed February to July 2014 and completed simultaneously when the gutters were installed thereby excluding precipitation fully. In order to isolate the hydrology on a plot basis, soil trenches to 60 - 100 cm depth were created around 0.16 ha plots with a ditch-witch, lined with 1m plastic and backfilled to block lateral water flow between plots in March 2014. The panels (1.4 x 2.2 m of each panel) were made of wood (Douglas-fir 5 x 5 cm), and UV resistant plastic (0.3 mm, Americover) were installed approximately 1.2 m above ground height; the height of panels varied to connect gutters and move water off the site. The panels covered approximately 0.072 ha, around 40 % of each plot (Figure 2). The panels prevented rainfall from reaching soils, generating artificial drought on the sites (i.e., throughfall exclusion TFE). In order to prevent panel-induced temperature differences between plots, similar panels were installed (on the Control: CON and Thinning: TH plot treatments) with holes which enabled rainfall to reach soils. Therefore, around 40 % of rainfall reduction occurred on the TFE plot and combination plot (THTFE) compared to the CON plot and the TH plot only. Five target trees in each core plot were selected for physiological measurements. After three years of drought treatment from June in 2014 to February in 2017, the artificial drought treatment (panels and gutters) were removed in March in 2017.

Measurements

Environmental Measurements

Environmental monitoring equipment documented changes in the treatment environment through time following throughfall panel installation. Campbell Scientific data-loggers (CR 1000) were used to monitor abiotic conditions on each of the 4 plots. One temperature and relative humidity sensor (CS215, Campbell Scientific, Inc.) were installed at 1 m height; a second temperature and relative humidity sensor (50 cm above ground) were set up under a panel near the center of each plot. Soil moisture content was monitored using a combination of time domain reflectometers and gypsum-block water potential sensors, a total of 8 sensors were used per plot. Two soil moisture sensors (CS620, Campbell Scientific, Inc), one under the panels and another outside panels, and five soil water potential sensors (253-L, Campbell Scientific, Inc), three under the panels and two other sensors outside panels, were buried at -20 cm soil depth, and one soil water potential sensor was buried at -60 cm and -1 m soil depth on each plot. A tipping bucket rain gage (TE525, Campbell Scientific, Inc), temperature, relative humidity (Hmp60), and solar radiation (CS300, Campbell Scientific, Inc) sensors were set up on top of a tower installed adjacent to the stand, above the trees of an 18 year-old plantation. Data were recorded and saved on the data-loggers every 30 minutes.

Sapflow density measurement

Five sample trees in each plot were instrumented with 20 mm Granier sapflow sensors installed in the outermost sapwood at 1.3 m height (Granier 1987). Each sensor had two probes (one heat probe and another reference probe), and these were inserted on the north-facing side of each tree and covered with an insulated refelective foam cone to avoid heating from sunlight. A heated upper probe and lower reference probe were separated by 12 cm of distance following

Granier (1987). A constant power of 0.2 W was delivered to the heated probe, while the lower probe was unheated to measure wood temperature. The main power gave constant 12-V to the entire system, and the current was adjusted to 0.140A. Sapflow density was calculated according to the formula (Eq 1) (Goulden and Field 1994; Granier 1987). All data from sapflow sensors were recorded using Campbell Scientific AM16/32 multiplexers and CR1000 data-loggers (Campbell Scientific, Logan, UT). Each reading from all the sensors was recorded and saved on the data-loggers every 30 minutes.

$J_s = 119 \times 10^{-6} [(\Delta T_{max} - \Delta T) / \Delta T]$ ^ 1.231   Eq (1);

Where, J_s represents sapflow density. ΔT_{max} is maximum temperature difference established between the heated and reference probes at zero flux, and ΔT is temperature difference between the heated and reference probes at positive flow condition.

DBH Increment

Point dendrometers were installed at 1.3 m height on the east side of the same trees as sapflow sensors. Automatic point dendrometers measured changes in the radius of the main stem with a rod held against the outside surface by a constant force; readings were recorded and saved on dendrometer data-loggers every 30 minutes (Agricultural Electronics Corporation, Arizona, USA). The length of stem growth in each year was calculated with the difference between two points ($P_2 - P_1$); 1) P_1: The starting point of rapid growth, and 2) P_2: The point of stem growth at the Peak during the growing season.

Predawn (Ψ_{pre}) and Midday water potential (Ψ_{mid}) measurement

Ψ_{pre} and Ψ_{mid} were measured using two pressure chambers (PMS, Instrument Corp., Corvallis, OR, USA). Branch samples from the middle of canopies in open areas were collected from newer foliage from trees (~25 m) using a shotgun, from branches located in and visually identified as sun foliage prior to measurement. Nine samples from target trees on each plot (treatment) were measured. $\Psi_{\text{pre and}}$ Ψ_{mid} measurements were conducted from 3:00 to 5:00 am and 12:00 to 15:00 pm, respectively on a warm, sunny day in July 2016.

Photosynthetic light response curve measurements

Photosynthetic light curve measurements were measured with a portable gas exchange system (Li- 6400XT, Li-Cor, Inc., Lincoln, NE). Sample branches were collected at the same time as leaf water potential measurements. The measurements were conducted from 10:00 am to 15:00 pm in July 2016. Three samples per treatment were chosen, brought down, and stem re-cut under water (McDowell et al. 2003). Flow rate, block temperature, and air humidity were set to 400 µmol s^{-1}, 27 °C, and 75 - 80 %, respectively. Light curves were created setting the photosynthetically active photon flux density (PPFD) ranged from 2000 to 0 µmol m^{-2} with nine incremental reductions: 2000, 1500, 1000, 800, 500, 250, 100, 50, and 0. Light compensation point, light saturation point, and the maximum net photosynthesis rate were estimated and calculated. Projected surface area of the measured needles was estimated using measurements of needle numbers.

Leaf Area Index measurement

Leaf area index (LAI: leaf area per ground area, m^2 m^{-2}) was measured at 1.2 m height using a circular fisheye lens (Lensbaby circular fisheye lens) and a digital camera (Nikon E990). Measurements were conducted at five points (Center, North, South, East, and West area) of each core plot. These measurements were taken three times in February 2014 (before thinning), April 2014 (after thinning), and in August 2018. The hemispherical photos were analyzed using Gap Light Analyzer soft program to calculate LAI (GLA version 2.0) (Frazer et al. 1999).

Statistical analysis

Significance tests for difference in photosynthetic light response, leaf water potential, and stem increments by treatments were performed using two-way ANOVA. Data of the sapflow density (J_s), soil volumetric water contents (VWC) and soil water potential (SWP) were averaged by treatments, year and month, then were analyzed using two-way ANOVA with repeated measures. Tukey multiple comparisons of means were used to compare the differences of each variable. All tests were carried out using R (version, 3.4.4).

Results

General climate and precipitation, and site-specific RH, air temperature (T_A), and VPD

The annual precipitation on the site in 2014, 2015, 2016, 2017, and 2018 was 526.8, 1342.4, 1068.9, 994.1, and 618.1 mm, respectively (Note: 2015, 2016, and 2017 are annual; partial years June to December in 2014, and January to October in 2018) (Figure 2, and table 2). Although the yearly total precipitation in 2015 was the highest during the entire research period, the summer precipitation (74.7 mm) from June to September was the lowest in 2015. The highest summer precipitation was 189.2 mm in 2016. The mean T_A during the research period was 10.1 °C, and the max. of T_A was 34.4 °C, and min. of T_A was -7.8 °C. The mean solar radiation was 0.14 kW m^{-2} over all five years, ranging from 0 to 1.45 kW m^{-2}. The annual precipitation over the 5-year study period was less than the yearly mean precipitation for 20 years compared to the nearby Buckley station (1214.1 mm) except in 2015. Summer precipitation was also lower during the study period (NOAA). The mean summer precipitation for the 5 years was 120.1 mm on the site, about 70 mm less than that from Buckley station average (196.6 mm). The 2015 and 2017 summer precipitation was well below and temperatures above average (Table 2).

Air temperature (T_A) was not significantly different among treatments except during summer seasons, where T_A was the highest on the TH plots (18.4 ℃) and the lowest on the CON plots (17.4 ℃) ($p<0.05$). The T_A showed no significant differences on the TH and THTFE plots from the panel installation, but the CON and TFE plots had higher T_A outside panels than under panels ($p<0.05$;Figure 3b). Mostly, T_A outside panels was warmer, ranging from 0 to 0.4 ℃ higher across four plots. RH among the four plots did not show significant differences except during winter seasons, the TH plot had the highest RH value across four plots while RH on the TFE was the lowest ($p<0.05$). RH and VPD were not significantly different between under and outside panel measurements, yet RH outside panels was lower than that under panels by 1.1 %, and VPD outside panels was higher than that under panels by 0.03 KPa. RH and VPD ranged from 21.1 to 100 % and 0 to 3.84 KPa across four plots, respectively (Figure 3a and 3c). The TH plot had the highest RH (87.2 %) with the lowest VPD (0.25 KPa) on average. In contrast, the TFE plot had the lowest RH (84.9 %) with the highest VPD (0.28 KPa) on average.

Soil water potential (Ψ_{soil})

Overall soil water potential (Ψ_{soil_A}): monthly soil water potential in the TFE plot generally had the lowest value among four plots before the removal of the panel in March 2017 (Figure 4a; n=5), and showed a significant difference among the four plots in 2014 and 2016 ($p<0.05$). The lowest value was -0.37 MPa on the TFE plot in October 2015. After panel removal Ψ_{soil_A} on the CON plot had the lowest value among the four plots ($p<0.05$). The drought treatment only affected Ψ_{soil_A} before the removal, however after panel removal, only the thinning treatment had an influence on Ψ_{soil_A} (Table 3, and 4). Over all years, the TH plot had the highest value of Ψ_{soil_A} across four plots.

Soil water potential differed between measurements under panels ($\Psi_{\text{soil\_U}}$) and outside panels ($\Psi_{\text{soil\_O}}$). We found that the $\Psi_{\text{soil\_U}}$ of TFE and THTFE under panels (n=3), were lower than those of $\Psi_{\text{soil\_A}}$ before the removal of the panels (Figure 4b). $\Psi_{\text{soil\_O}}$ (-0.58 MPa) was the lowest on the TFE plot in Oct in 2015. After the removal of panels, $\Psi_{\text{soil\_U}}$ on the CON plot had the lowest value among the treatments. The $\Psi_{\text{soil\_U}}$ had a similar pattern with $\Psi_{\text{soil\_A}}$ overall.

Soil volumetric water contents (VWC)

The TFE plot had the lowest VWC during the research period, while the TH plot had the highest VWC throughout the years (Figure 5a). The thinning effect on VWC is clear in 2014 and 2015 for the non-growing season ($p<0.05$), yet there was no effect of thinning on VWC in the two subsequent years (in 2015, and 2016) when accounting for month (Table 4). After the removal of panels, VWC increased in both under and outside panels (Figure 4b-c) despite less rainfall (1068.9 mm) in 2017 compared with previous years (994.1 mm in 2015 and 618.1 mm in 2016), and VWC on the TH plot was highest in 2017 and 2018 among treatments ($p < 0.05$).

Tree physiological responses

Leaf area index (LAI)

LAI was measured three times during the research period from 2014 to 2018. LAI among the four plots was not different before thinning, but after thinning, with significant difference ($p<0.05$), the values were reduced to 1.94 from 2.48 and 2.06 from 2.49 on the TH and THTFE plots in 2014, respectively (Table 1). LAI was measured again in summer 2018, and we found that LAI on the two thinned plots partially recovered (2.30 on the TH and 2.39 on the THTFE), while LAI on the TFE plot was reduced to 2.24 in 2018 from 2.49 in 2014.

Sapflow density (J_s)

TFE reduced sapflow density (J_s) in comparison to the CON plot, and TH increased J_s compared to the CON plot from 2014 to 2016. For three summers, there was ~20 % increase in J_s by thinning in comparison to in the CON plot and ~28 % reduction of J_s in TFE plot compared to the CON plot. After the TFE treatment was removed, the thinning treatment still had increased J_s, and the drought treatment TFE J_s was similar to the TH and THTFE treatments (Figure 6). Overall, the TH plot had the highest J_s for the five years, and J_s on TFE plot was lowest before drought treatment removal, after panel removal J_s on the CON plot became the lowest 2017 to 2018. The monthly summer mean of J_s (from June to September) by year showed significant difference among plots (Table 5) ($p<0.05$). Notably J_s in 2014 and 2015 were generally higher across all four treatments, then gradually decreased through time.

Photosynthesis and stomatal conductance (g_s)

Thinning and throughfall exclusion treatments affected photosynthesis ($A_{\max}$; $p<0.05$), yet there were no interactive effects between thinning and TFE on photosynthesis (Figure 7). $A_{\max}$ was increased by ~50.1 % by thinning, but $A_{\max}$ decreased by ~33.0 % with throughfall exclusion compared to the CON. Photosynthesis on the TH plot was the highest among four plots, while the TFE plot showed the lowest photosynthesis. Photosynthesis on two plots with thinning treatments were higher than on the CON plot. Stomatal conductance (g_s) displayed a similar trend as photosynthesis. On the TH plot, g_s was the highest among the four plots and the lowest on the TFE plot over the series of light intensity. Thinning only influenced g_s ($p<0.05$), that is there were no significant differences between treatments related to throughfall exclusion (Table 6).

Predawn water potential (Ψ_{pre}) and midday water potential (Ψ_{mid})

Both Ψ_{pre} and Ψ_{mid} exhibited similar trends with higher water potential in the thinned treatments. Ψ_{pre} and Ψ_{mid} were highest in TH plot, and lowest in TFE plots. Ψ_{pre} and Ψ_{mid} in the TH plot were -0.66 MPa and -0.90 MPa, respectively (Figure 8). Ψ_{pre} and Ψ_{mid} on the TFE were lower -0.78 MPa and -1.61 MPa, respectively. Thinning and drought effected Ψ_{mid} ranked highest to lowest: TH>THTFE>CON>TFE, but there was no interactive effect ($p<0.05$). However, the thinning and interactive effects on Ψ_{pre} were observed ($P<0.05$).

Stem increments

Stem increments were measured with dendrometers from Jun in 2014 to Nov in 2017. Three years of stem increments exhibited the same trend as other physiological traits, in that the TH plot had the highest stem increments and stem increments on the TFE plot were lowest. Thinning increased stem growth by 24.7 % on average, while throughfall exclusion decreased growth 34.1% on average over the course of three years from 2015 to 2017. The thinned plot had a stem expansion period of ~ 1 month longer than on the other plots (Table 7), and drought extenuated the difference in the length of the growing season reduction from TFE. The effect of thinning on stem increments was detected over the course of three years, yet the effects of drought and interaction were independent in 2015 and 2017, respectively ($p<0.05$;Figure 9).

Discussion

In this study, two treatments; 1) thinning, and 2) throughfall exclusion, influenced the soil water potential, sapflow density, photosynthesis, stem growth and leaf water potential of Douglas-fir but interactive effects between two treatments were not present for most results. Thinning enhanced stem growth, soil water potential, sapflow density and leaf water potential, while throughfall exclusion decreased them. The combination of thinning and throughfall exclusion treatment showed thinning could mitigate the drought effects on tree physiology and stem growth. This study reveals that silvicultural applications such as thinning can mitigate drought effects on tree growth and physiology.

Effects of Treatments (Thinning and Throughfall exclusion) on microclimate and soils

We expected T_A under panels would increase regardless of the type of panels (two types of panels; 1) wood frame with tarp on TFE and THTFE plots, and 2) tarp panels with water distributed back on CON and TH plots), yet the panels decreased the $T_{A.}$ This result differs from other throughfall exclusion research which found both air temperature and the soil temperature increased under panels (Pangle et al. 2012). The panels blocked or reflected sunlight rather than keeping the energy, likely a result of ultraviolet resistant plastic used (to extend panel life). Thinning also had an influence on $T_{A,}$ while the T_A outside panels was higher than under panels on both the CON and TFE, there was no differences of T_A on the two thinned plots in response to panel installation. Thinning enabled more light energy to reach the ground due to reduced canopy cover, allowing the T_A under panels to increase — perhaps allowing greater ground circulation. The panels changed the spatial pattern of soil moisture due to the positioning of panels, similar to other studies (Fay et al. 2000; Hanson 2000; Pangle et al. 2012). The soil water potential and soil water contents were lower under the panels than the areas not covered by panels, particularly on sites equipped with excluding panels and gutters (Figure 4b, and 4c). Far from our expectations, the throughfall exclusion panels were not able to generate severe drought on the sites, given moderated drought (-0.6 MPa: the lowest on the TFE plot) under panels. The lowest value was still higher than the expected wilting point (- 1.5 MPa) (Brady and Weil, 2002), indicating the study site to be relatively mesic with abundant soil water at deeper soil levels. Probes at deeper levels revealed the lowest soil water potential deeper in the soil (-60 cm to -1 m) was still relatively high (-0.47 MPa) on TFE plot (note: study design limited to one sensor/plot at these depths). Yet the average across four plots was -0.19 ± 0.09 MPa at deeper soil depths. Despite our efforts to select a local convexity where we anticipated we could limit water inputs, the system remained relatively mesic even during extreme drought periods in 2015 and 2017.

Tree responses to treatments

We observed increased photosynthesis in both the TH and THTFE plots due to higher stomatal conductance, higher CO_2 uptake (>1.5x g_s on thinned sites) and greater soil water availability (McDowell et al. 2003). Thinning also removed canopy cover (Table 1), and therefore less competition for light and nutrients to remaining trees by thinning may also have increased photosynthesis (Briggs et al 2000). Lewis et al. (2000) found that photosynthesis increased with light availability. Photosynthesis responded to combinations of thinning and throughfall exclusion with A_{max} on TH>THTFE>CON>TFE; photosynthesis on the thinning treatment more than compensated for the effects of throughfall exclusion (i.e., A_{max} THTFE>CON; Table 6). We measured Ψ_{pre} as an indicator of soil water availability during a warm and sunny period in July 2016. The lowest water potential Ψ_{pre} was found on the TFE, with the highest water potential on the TH, consistent with other studies of thinning response (Aussenac and Granier 1988). Our Ψ_{pre} was similar on the TH and THTFE sites suggesting nighttime water recovery at low stocking, however the fully stocked stands had significantly lower water availability which supports the idea that both higher stocking and throughfall exclusion increased drought. Our Ψ_{mid} results corresponded with previous research which showed Ψ_{mid} on thinned stands had higher values compared to control (Bréda et al. 1995; Stoneman et al. 1997), and our Ψ_{mid} showed increasing water potential from lowest TFE<CON<THTFE<TH to highest consistent with water stress related

to competition and throughfall exclusion. This result is useful in understanding stand responses to thinning as some have observed the opposite result with Ψ_{mid} on a thinning treatment with the lower water potential probably due to crown exposure to higher solar radiation (Brix and Mitchell 1986). Sapflow densities on both TH and THTFE plots were increased by the thinning treatment during the summer immediately following thinning in 2014. The response in 2014 would have had a minimal effect of the throughfall exclusion panels which became operational (gutters installed), on TFE and on THTFE in July. This difference in installation likely affected sapflow density on THTFE plot in 2014; no throughfall exclusion effect was found on THTFE plot in 2014. The sites were subjected to a severe drought in 2015 (NOAA), this drought generally decreased sapflow density across all plots in comparison with 2014. Thinning increased sapflow densities on the TH and THTFE in 2015 and 2016, particularly early in the growing season due to greater water availability, and differences from thinning became less pronounced in August when all plots were under greater water stress. The long-term effects of the 2015 drought carried through the study completion in 2018, and show the importance of thinning in increasing early growing season sapflow (Table 5).

Higher sapflow density with thinning also translated into greater stem growth. Dendrometers show earlier growth initiation, later growth cessation and greater overall growth rate with thinning and the opposite impacts on growth with throughfall exclusion (Figure 10). Gessel et al. (1990) stated stem growth at a nearby site started in the middle of April. We found that stem growth started in the middle of April on unthinned sites, yet in early March on thinned sites in this study (Figure 10). We also detected that the number of days of stem increment expansion was also responsive to treatment. The TH plot grew for 25 more days than those on other plots during the 2015 and 2017 droughts (Table 7), consistent with prolonged soil water availability. Precipitation and/or soil water availability during Spring are positively correlated with Douglas-fir growth (Brubaker 1980; Littell et al. 2008), which is consistent with early initiation of stem growth. Thinning induced the stem increment, and the effect of thinning lasted until 2017. Our results suggest less competition for water (more soil water availability), is a primary driver of stem increment, and the TH plot was higher than on the CON plot through 3 years from 2015 to 2017, even during the drought year of 2015 (Figure 9).

The throughfall exclusion treatment reduced photosynthesis and stomatal conductance of Douglas-fir by 33.0 % and by 32.4 %, respectively. Also, midday and predawn water potential declined in response to lower water availability. These reductions of photosynthesis and stomatal conductance are likely due to stomatal closure to prevent water loss. In previous Douglas-fir studies, water stress reduced photosynthesis by 20-50 %, stomatal conductance by 40-70 %, and transfer conductance by 40-70 % (Warren et al. 2004); when plant water potential dropped to -1.6 MPa the photosynthesis rate declined ~ 30 % (Brix 1979), and a decrease in photosynthesis of Douglas-fir trees with an increase in water stress regardless of fertilization treatment was observed (Brix 1972). Our throughfall exclusion resulted in $\Psi_{\mathrm{mid}} < -1.6$ MPa on the TFE plot; another study, found stomata closure of Douglas-fir below -1.5 MPa (Warren et al. 2003), indicating our Douglas-fir were subjected to drought stress, even though the soil water potential suggests the drought was not severe on this site. Thinning mitigated the drought effects on tree physiology; the THTFE treatments showed better performance for photosynthesis, water potential, and sapflow density compared to the CON.

Water Recovery after throughfall exclusion removal

The drought treatments (panels and gutters) were removed from February to April in 2018. This removal of throughfall exclusion changed the pattern of sapflow density. Sapflow density on the CON rapidly decreased following panel removal, while sapflow density on the TFE increased, in contrast to the decrease in sapflow on the TFE from 2014 to 2016. Sapflow on the THTFE also increased in 2017 rapidly approaching saplow on the TH. There was a notable change in sapflow density between the CON and THTFE before and after panel removal. Sapflow of the CON and THTFE were similar in July and August from 2015 to 2016, but the sapflow diverged with the CON<THTFE following panel removal in July and August 2017 and 2018. The rapid sapflow recovery on the TFE treatment, following panel removal may be explained by an increase in root-to-shoot ratio or root expansion (rooting depth) during the drought treatment years from 2015 to 2016. Chan et al. (2003) found root biomass increased under water stress conditions with 3 year-old Douglas-fir seedlings. Fine root production in a Norway spruce forest in Southeast Germany also increased under mild drought treatment (-0.06 at soil water potential) of throughfall exclusion research (Gaul et al. 2008), a meta-analysis found root-to-shoot ratios from temperate and tropical regions increased under dry conditions (Mokany et al. 2006). A review of tree response to drought conditions, showed trees are inclined to produce more roots, therefore increasing water uptake, while regulating water loss from transpiration (Brunner et al. 2015).

Conclusion

Our research found that thinning increased sapflow density, photosynthesis, and water potential as well as DBH growth, while the throughfall exclusion treatment reduced tree physiological traits and DBH growth. We also observed that thinning could mitigate the effect of drought on tree growth and physiology.

Our throughfall exclusion did not create severe drought on this mesic, productive site. Yet artificially induced-moderate drought still had negative effects on tree physiology and growth;

these differences may have been enhanced by two natural droughts (2015 and 2017) which coincided with our study period.

Silvicultural thinning to below full-stocking (i.e., Curtis RD~41), mitigated the effects of drought on tree physiology and tree growth. Thinning also enhanced physiological traits and tree growth. In light of this research and others, silvicultural applications may serve to mitigate drought effects on tree growth and physiological responses in the future.

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Tables & Figures

Table 1. Site description before and after the thinning treatment. After thinning, around 33 % of stand density (SD) and 25 % of basal area (BA) were reduced, respectively. CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively.

Plot	CON	TFE	TH	THTFE
Before thinning				
SD (Trees ha^{-1})	494	506	419	419
Curtis RD	56.8	62.1	56.3	56.8
BA (m^2 ha^{-1})	54.3	52.3	50.8	52.6
DBH (cm)	36.6 ± 0.68	36.5 ± 0.58	38.9 ± 0.9	39.0 ± 0.8
Slope (%)	10~20	10~20	10~20	10~20
Elevation (m)	548	546	548	545
Aspect	S	S	S-W	S-W
LAI (2014)	2.52	2.49	2.48	2.49
After thinning				
SD (Trees ha^{-1})			275	288
Curtis RD			40.7	41.7
BA (m^2 ha^{-1})			38.2	39.2
DBH (cm)			42.1 ± 0.92	40.8 ± 0.84
LAI (2014)			1.94	2.06
LAI (2018)	2.53	2.24	2.30	2.39

Table 2. On-site yearly total precipitation and summer (Jun to Sep) total precipitation during the research period and Mean max and min. of air temperature. Total precipitation in 2014 was collected from June, and Total precipitation in 2018 was collected until October. Mean max and min. of air temperature in summer, total precipitation, and summer precipitation from Buckley station (1981 to 2010).

	2014	**2015**	**2016**	**2017**	**2018**
Mean of Max. Air. T (℃) (summer)	29.4	30.2	28.6	30.4	28.9
Mean of Min. Air. T (℃) (summer)	8.1	7.1	6.5	6.2	5.7
Max. Air T (℃) (summer)	34.4	32.3	31.5	32.2	31.1
Min. Air T (℃) (summer)	6.1	3.7	4.1	4.8	0.3
Total Preci. (mm) (year)	526.8	1342.4	1068.9	994.1	618.1
Preci. (mm) (summer)	144.9	74.7	189.2	88.1	103.9
Buckley station NCDC (1981 to 2010)					
Mean of Max. Air. T (℃) (summer)			23.2		
Mean of Min. Air. T (℃) (summer)			11.1		
Total Preci. (mm) (year)			1214.1		
Preci. (mm) (summer)			196.6		

Table 3. Summary of significant statistical differences in Sapflow density, Soil water potential (SWP), Soil volumetric water contents (VWC) during entire years. T, E, and I indicate Thinning, Throughfall exclusion, and interactive effect, respectively (*p*<0.05).

Year	Month	Sapflow	SWP	SM
2014	Jun	T		
	Jul	T		
	Aug	T, E		T, E, I
	Sep		E	
	Oct	T	E	
	Nov	T	E	
	Dec	T	E	
2015	Jan	T	E	T
	Feb	T		T, E
	Mar	T		E
	Apr	T		E
	May	T	E	E
	Jun	T, E	E	T, E
	Jul	T, E	E	
	Aug	E		
	Sep	E		
	Oct	T		E
	Nov	T		
	Dec			
2016	Jan		E	E
	Feb	T	T	
	Mar	T, E	T	
	Apr	T	T	
	May	T	T	T, E
	Jun	T, E	T, E	

	Jul	T, E	E	T
	Aug	T, E, I	E	T
	Sep	T, E	E	T
	Oct	E, I	E	
	Nov	T		T
2017	Apr			
	May	T		
	Jun	T		T
	Jul	T		T
	Aug	T		T
	Sep	T		T
	Oct			T
2018	Jun	T	T	T
	Jul	T	T	T
	Aug		T	T
	Sep			T
	Oct			T

Table 4. Statistical significance for the effects of Month, Throughfall exclusion (PA), and Thinning (TH) on Sapflow density (J_s), Soil volumetric water contents (VWC) at depth of 20 cm, and soil water potential (SWP) at depth of 20 cm for the entire research period (2014 to 2018). *** p<0.001; ** p<0.01; * p<0.05; · p<0.1

	J_s	VWC	SWP
2014			
TH	<0.001 ***	<0.05 *	0.493
PA	<0.01 **	0.204	<0.05 *
Month	<0.001 ***	<0.001 ***	<0.001 ***
TH:PA	<0.1 ·	0.560	0.484
TH:Month	0.221	0.943	0.465
PA:Month	0.543	0.184	<0.001 ***
TH:PA:Month	<0.05 *	0.605	0.673
2015			
TH	<0.001 ***	<0.1 ·	0.687
PA	<0.01 **	<0.05 *	0.107
Month	<0.001 ***	<0.001 ***	<0.001 ***
TH:PA	0.100	0.697	0.459
TH:Month	<0.001 ****	0.864	0.924
PA:Month	<0.05 *	<0.05 *	0.324
TH:PA:Month	0.846	0.997	0.697
2016			
TH	<0.001 ***	<0.1 ·	<0.1 ·

PA	<0.01 **	0.128	<0.05 *
Month	<0.001 ***	<0.001 ***	<0.001 ***
TH:PA	<0.05 *	0.488	0.705
TH:Month	<0.05 *	0.998	0.958
PA:Month	<0.05 *	<0.05 *	<0.001 ***
TH:PA:Month	0.775	0.918	0.899
2017			
TH	<0.05 *	<0.05 *	<0.05 *
PA	0.822	0.242	0.758
Month	<0.001 ***	<0.001 ***	<0.001 ***
TH:PA	0.184	0.781	0.351
TH:Month	<0.001 ***	0.311	0.711
PA:Month	0.151	0.488	0.465
TH:PA:Month	<0.1 .	0.981	0.865
2018			
TH	<0.1 .	<0.01 **	<0.05 *
PA	0.603	0.101	0.878
Month	<0.001 ***	<0.001 ***	<0.001 ***
TH:PA	0.341	<0.001 ***	0.362
TH:Month	<0.001 ***	<0.05 *	0.596
PA:Month	0.717	0.102	0.998
TH:PA:Month	0.544	<0.001 ***	0.998

Table 5. Monthly mean ± 1 SE of sapflow density (J_s) in summers for entire research period for Control (CON), Throughfall exclusion (TFE), Thinning (TH), and Combination (Thinning and Throughfall exclusion; THTFE)

Plot	Month	2014	2015	2016	2017	2018
CON	Jun	3.1 ± 0.0 $^{(a)}$	3.1 ± 0.2 $^{(a)}$	2.3 ± 0.2 $^{(ab)}$	1.7 ± 0.2 $^{(b)}$	2.0 ± 0.3 $^{(b)}$
	Jul	4.9 ± 0.4 $^{(a)}$	3.0 ± 0.4 $^{(b)}$	3.4 ± 0.3 $^{(b)}$	2.3 ± 0.3 $^{(b)}$	2.7 ± 0.4 $^{(b)}$
	Aug	4.4 ± 0.3 $^{(a)}$	1.7 ± 0.4 $^{(c)}$	3.2 ± 0.1 $^{(ab)}$	1.5 ± 0.3 $^{(c)}$	2.1 ± 0.4 $^{(bc)}$
	Sep	2.7 ± 0.3 $^{(a)}$	1.1 ± 0.2 $^{(b)}$	2.1 ± 0.2 $^{(ab)}$	0.9 ± 0.2 $^{(b)}$	2.1 ± 0.6 $^{(ab)}$
TFE	Jun	2.6 ± 0.1^{ns}	2.6 ± 0.2 ^{ns}	1.7 ± 0.2 ^{ns}	2.0 ± 0.3 ^{ns}	2.3 ± 0.0 ^{ns}
	Jul	3.3 ± 0.3 ^{ns}	2.4 ± 0.4 ^{ns}	2.6 ± 0.3 ^{ns}	3.3 ± 0.4 ^{ns}	3.0 ± 0.1 ^{ns}
	Aug	3.3 ± 0.2 $^{(a)}$	1.1 ± 0.2 $^{(b)}$	2.1 ± 0.1 $^{(ab)}$	2.6 ± 0.6 $^{(ab)}$	2.6 ± 0.2 $^{(ab)}$
	Sep	1.9 ± 0.2 $^{(ab)}$	0.7 ± 0.1 $^{(b)}$	1.2 ± 0.2 $^{(ab)}$	1.3 ± 0.3 $^{(ab)}$	2.2 ± 0.1 $^{(a)}$
TH	Jun	3.5 ± 0.3 $^{(b)}$	4.8 ± 0.1 $^{(a)}$	2.8 ± 0.2 $^{(ab)}$	2.9 ± 0.4 $^{(ab)}$	3.8 ± 0.2 $^{(b)}$
	Jul	5.7 ± 0.9 $^{(a)}$	4.6 ± 0.3 $^{(ab)}$	4.0 ± 0.2 $^{(b)}$	4.2 ± 0.6 $^{(b)}$	4.4 ± 0.5 $^{(b)}$
	Aug	5.1 ± 0.4 $^{(a)}$	2.3 ± 0.4 $^{(c)}$	3.4 ± 0.2 $^{(b)}$	2.9 ± 0.2 $^{(bc)}$	2.6 ± 0.1 $^{(bc)}$
	Sep	2.7 ± 0.3 $^{(a)}$	1.4 ± 0.2 $^{(b)}$	2.3 ± 0.1 $^{(ab)}$	1.8 ± 0.0 $^{(b)}$	2.1 ± 0.0 $^{(b)}$
THTFE	Jun	3.4 ± 0.2 $^{(a)}$	3.5 ± 0.5 $^{(a)}$	2.6 ± 0.2 $^{(b)}$	2.8 ± 0.5 $^{(ab)}$	3.5 ± 0.3 $^{(a)}$
	Jul	5.5 ± 0.2 $^{(a)}$	3.1 ± 0.5 $^{(b)}$	3.4 ± 0.2 $^{(ab)}$	3.8 ± 0.5 $^{(ab)}$	3.8 ± 0.4 $^{(ab)}$
	Aug	4.8 ± 0.3 $^{(a)}$	1.6 ± 0.3 $^{(c)}$	3.2 ± 0.7 $^{(b)}$	2.8 ± 0.2 $^{(bc)}$	2.6 ± 0.0 $^{(bc)}$
	Sep	3.0 ± 0.3 $^{(a)}$	0.9 ± 0.3 $^{(b)}$	2.0 ± 0.3 $^{(a)}$	1.5 ± 0.1 $^{(ab)}$	2.3 ± 0.0 $^{(a)}$

Different letters indicate significantly different means (n=5) (p<0.05). ^{ns} indicates no significant differences. The difference in the same month by different years was tested.

Table 8. Net photosynthesis (A_{max}) and stomatal conductance (g_s). Each value is the mean of 3 samples. Error bars represent (± 1 SE) of the mean. Control (CON), Throughfall exclusion (TFE), Thinning (TH), and Combination (Thinning and Throughfall exclusion; THTFE).

Treatment	A_{max}	g_s
CON	11.3 (0.9) ^{bc}	0.13 (0.02) ^{b}
TFE	8.2 (0.8) ^{c}	0.08 (0.01) ^{b}
TH	16.9 (0.3) ^{a}	0.26 (0.10) ^{a}
THTFE	14.7 (0.2) ^{a}	0.20 (0.03) ^{a}

Different letters by treatments indicate significantly different means ($p<0.05$).

Table 7. Days of expansion in stem increment from 2015 to 2017. Stems started growing on the middle of April in 2015, except on TH where stem growth began in early March in 2015. However, from 2016 to 2017, stem among four plots started to grow in early or middle of April. Each value is the mean of 3 samples. Error bars represent (± 1 SE) of the mean. Control (CON), Throughfall exclusion (TFE), Thinning (TH), and Combination (Thinning and Throughfall exclusion; THTFE)

	2015	2016	2017
CON	97 (0.9) ^{b}	118 (9.2) ^{ns}	103 (1.8) ^{bc}
TFE	89 (0.6) ^{c}	113 (1.3) ^{ns}	90 (5.2) ^{c}
TH	125 (2.3) ^{a}	128 (2.6) ^{ns}	129 (0.6) ^{a}
THTFE	97 (0.6) ^{b}	122 (3.5) ^{ns}	109 (5.7) ^{b}

Different letters indicate significantly different means (n=3) (p<0.05). ^{ns} indicates no significant differences.

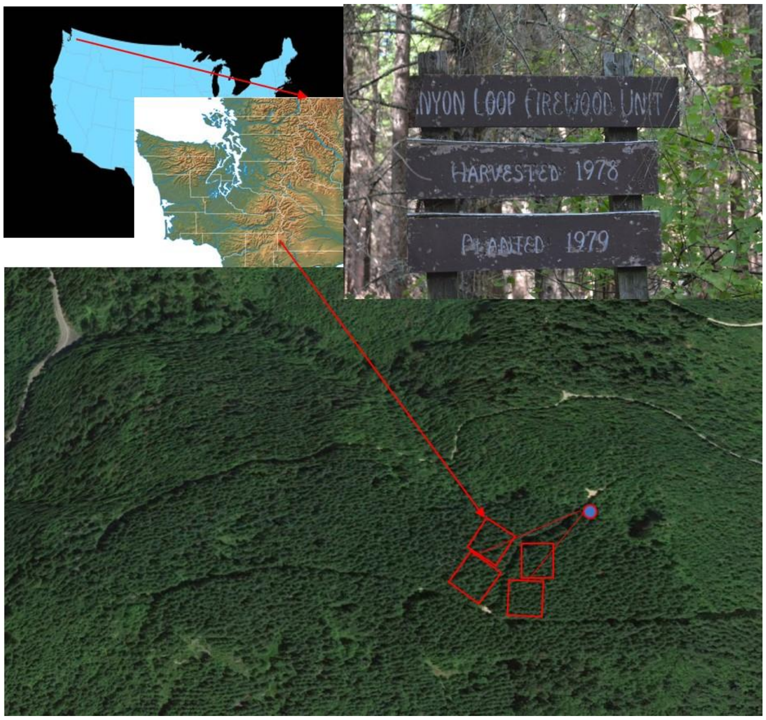

Figure 1. The location of study site at Experimental forest at UW (Pack Forest), Canyon Loop Firewood stand. Four red squares indicate plots and the blue dot represents a weather station at an open area (tower).

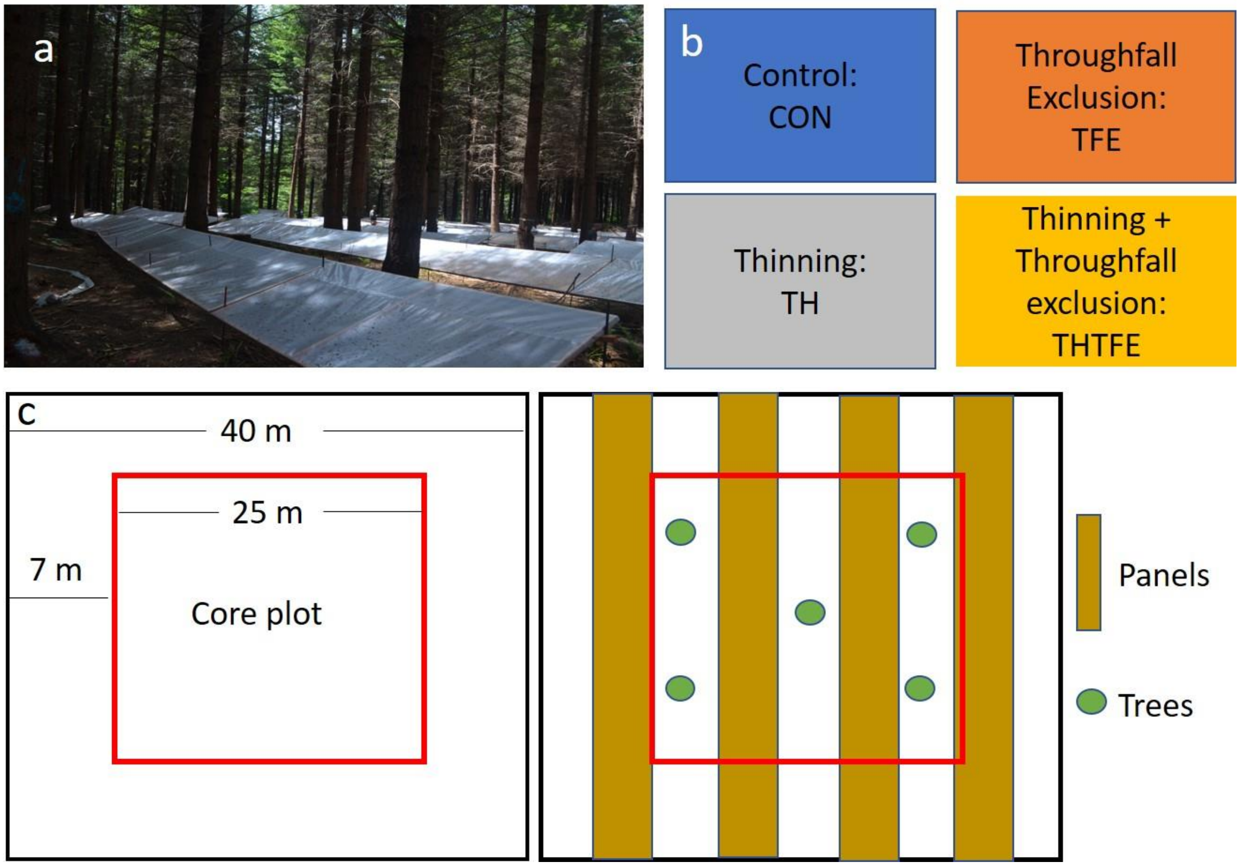

Figure 2. **Throughfall exclusion panels (a), Experimental design (b), and site layout (c)**

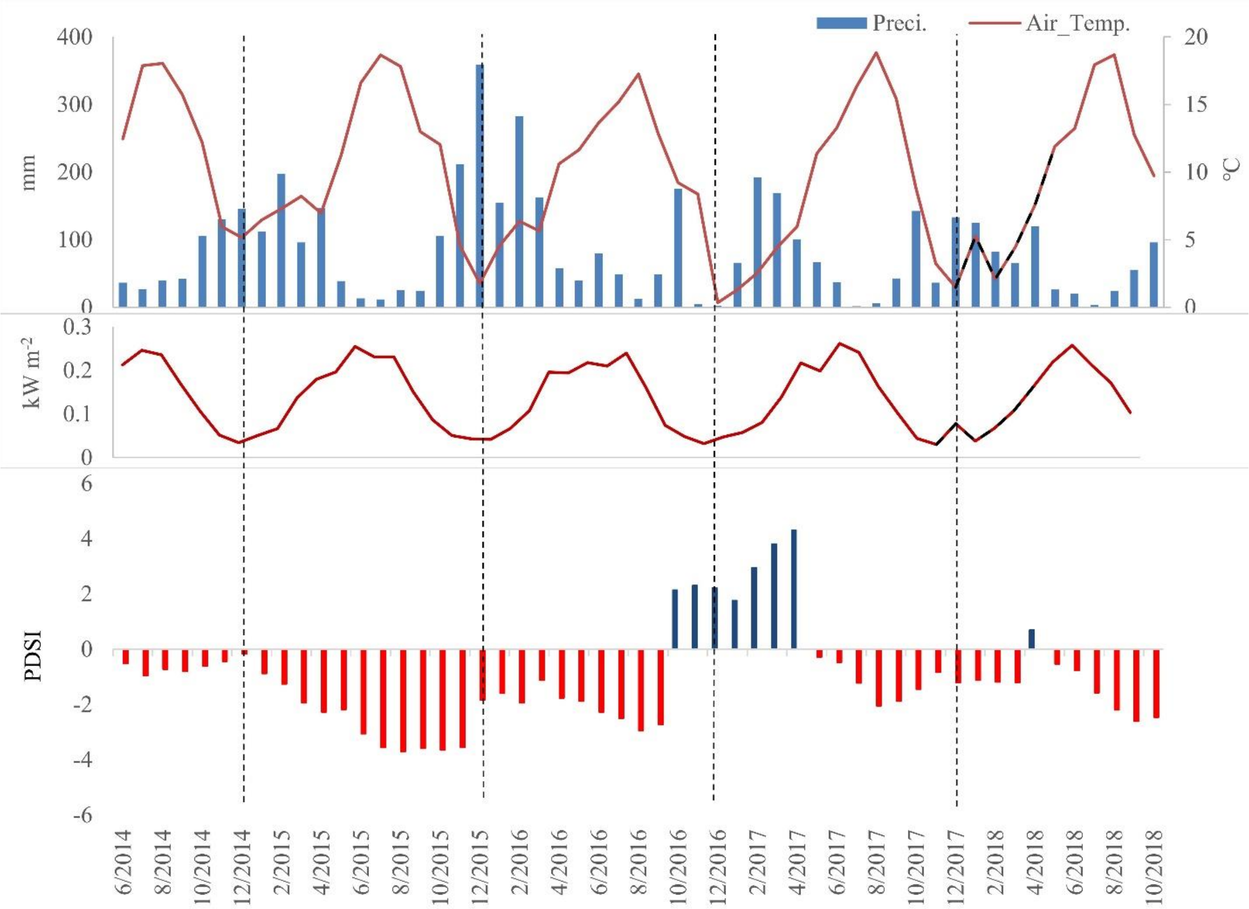

Figure 3. Environmental data from the weather station on the tower. a) Monthly mean air temperature and monthly precipitation during the research period. b) Monthly solar radiation during the research period. Dash line on Air temp. from December 2017 to May 2018 indicates estimated data. c) Palmer drought severity index (NOAA).

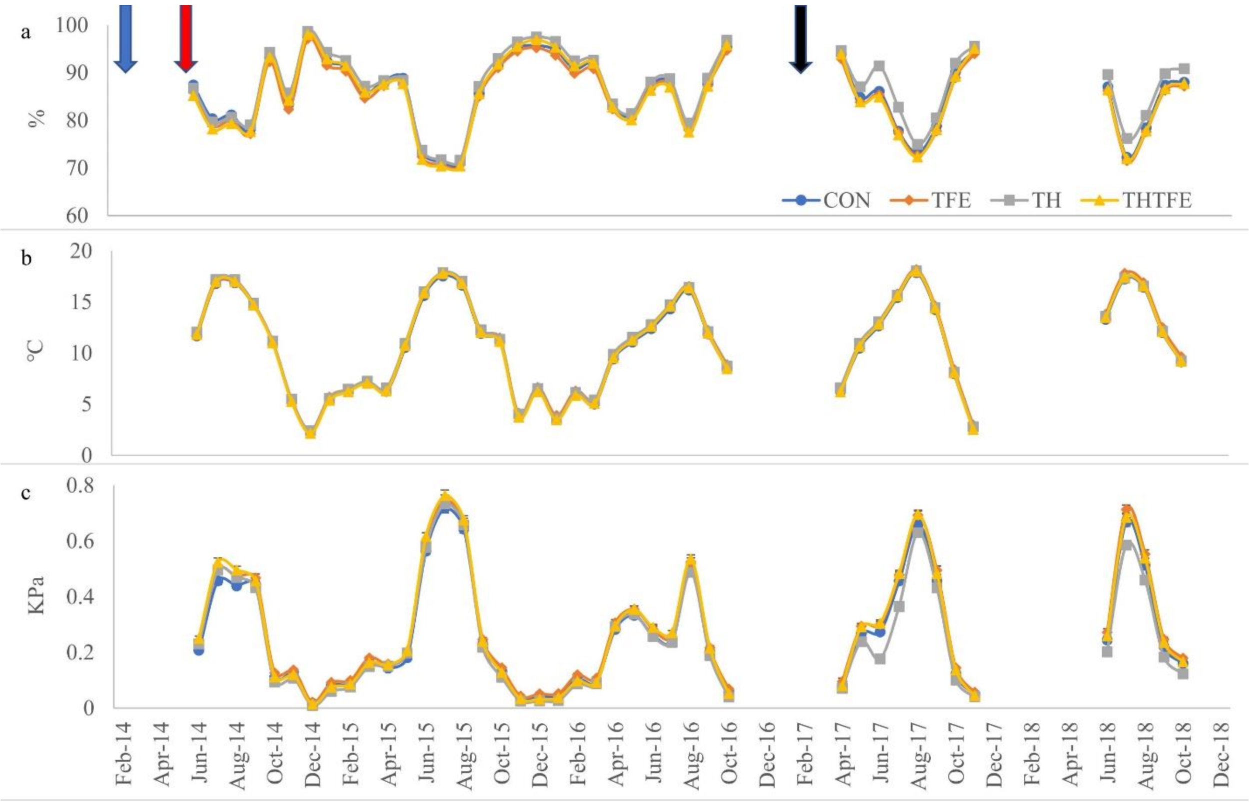

Figure 4. Monthly means of relative humidity (RH), air temperature, and vapor pressure deficit (VPD). a) RH, b) air temperature, and c) VPD. The first arrow, second arrow, and third arrow (from left) indicate thinning, panel installation, and panel removal, respectively. Data lost in winters in 2016 and in 2017 due to battery issues. CON: Control; TFE: Throughfall exclusion; TH: thinning; and THTFE: Combination (Thinning and Throughfall exclusion).

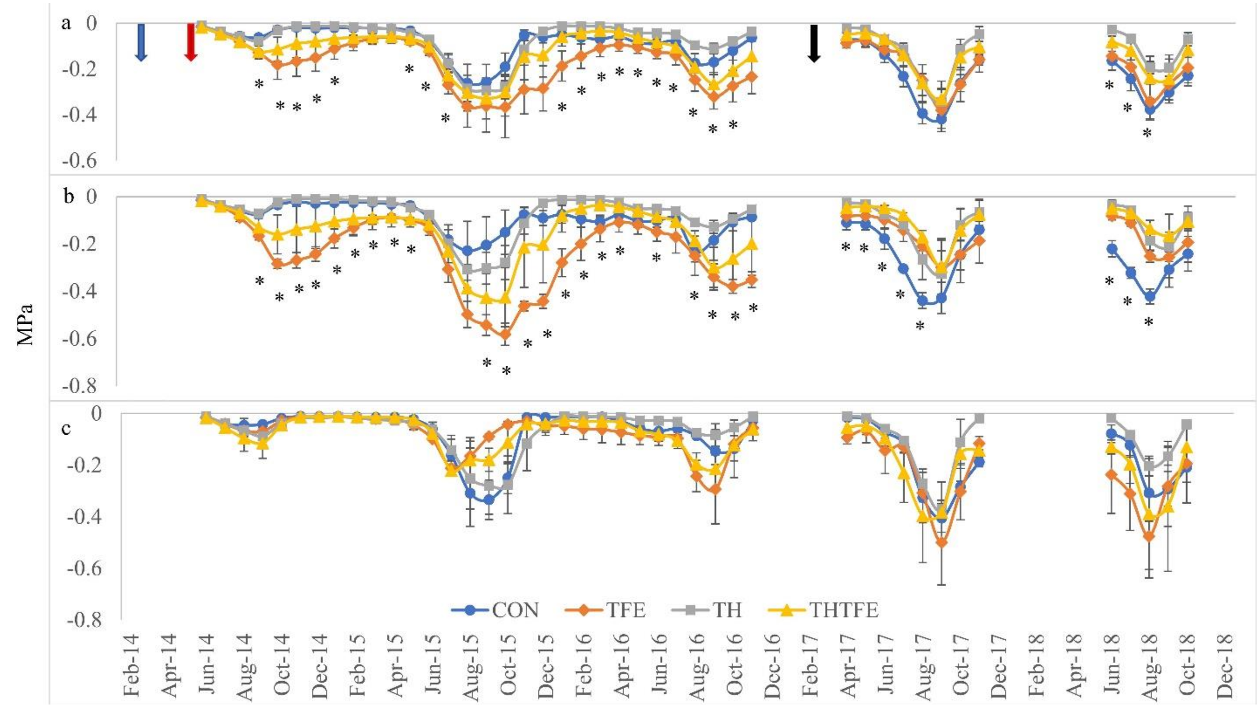

Figure 5. Monthly mean of Soil water potential (SWP) at -20 cm depth. a) Mean of SWP (n = 5), b) Mean of SWP under panels (n=3), and c) Mean of SWP outside panels (n=2). The first arrow, second arrow, and third arrow (from left) indicate thinning, panel installation, and panel removal, respectively. Data lost in winters in 2016 and in 2017 due to solar panels failed to recharge batteries. CON: Control; TFE: Throughfall exclusion; TH: thinning; and THTFE: Combination (Thinning and Throughfall exclusion). Analyzed with two-way ANOVA with repeated measure. *indicates significant differences among treatments (*p* < 0.05).

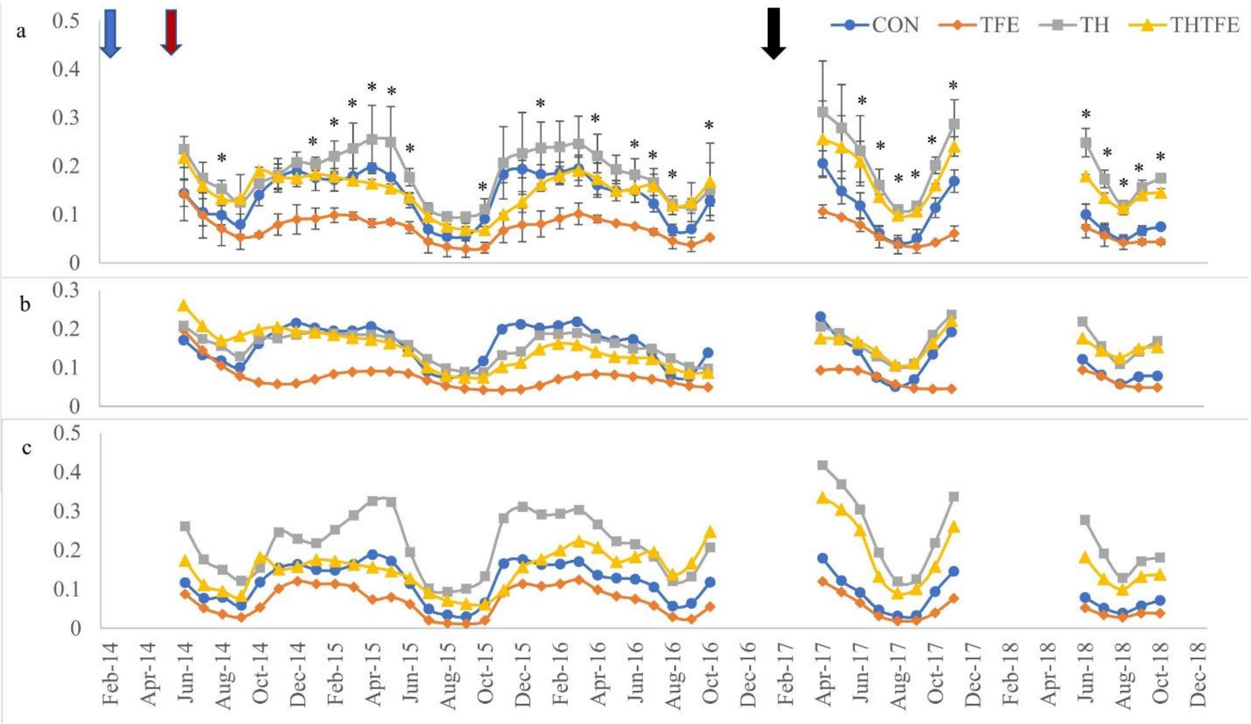

Figure 6. Monthly mean of Soil volumetric water contents (VWC) at -20 cm depth. a) Mean of VWC (n=2), b) Mean of VWC under panels (n=1), and c) Mean of VWC outside panels (n=1). The first arrow, second arrow, and third arrow (from left) indicate thinning, panel installation, and panel removal, respectively. Data lost in winters in 2016 and in 2017 due to solar panels failed to recharge batteries. CON: Control; TFE: Throughfall exclusion; TH: thinning; and THTFE: Combination (Thinning and Throughfall exclusion). Analyzed with two-way ANOVA with repeated measure. *indicates significant differences among treatments (*p*<0.05).

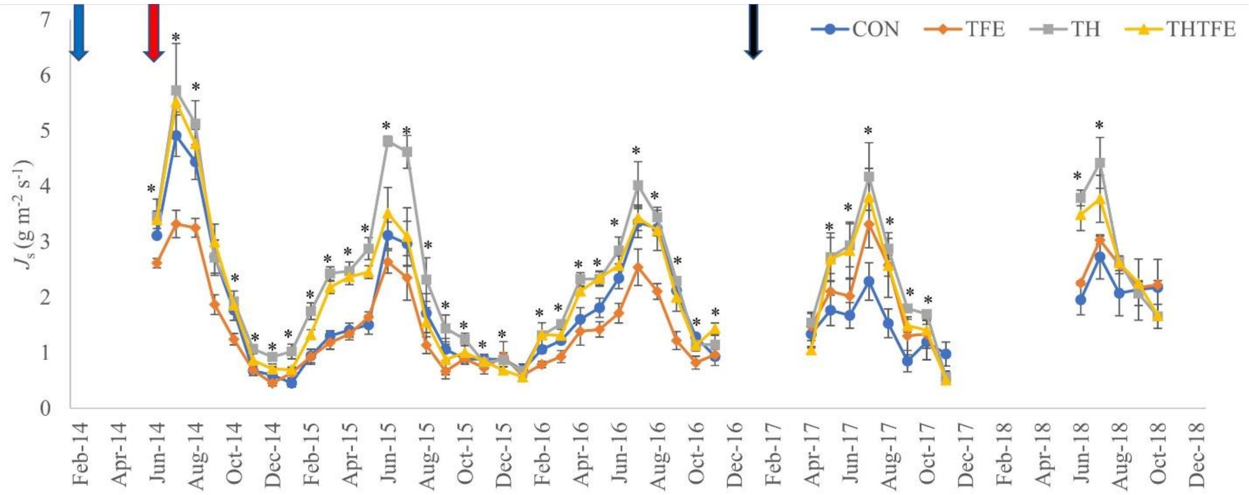

Figure 7. Monthly mean sapflow density fluctuation. The first arrow, second arrow, and third arrow (from left) indicate thinning, panel installation, and panel removal, respectively. Data lost in winters in 2016 and in 2017 due to solar panels failed to recharge batteries. Asterisks (*) represents significantly differences between treatments (p<0.05). CON: Control; TFE: Throughfall exclusion; TH: thinning; and THTFE: Combination (Thinning and Throughfall exclusion). Analyzed with two-way ANOVA with repeated measure. *indicates significant differences among treatments (p<0.05).

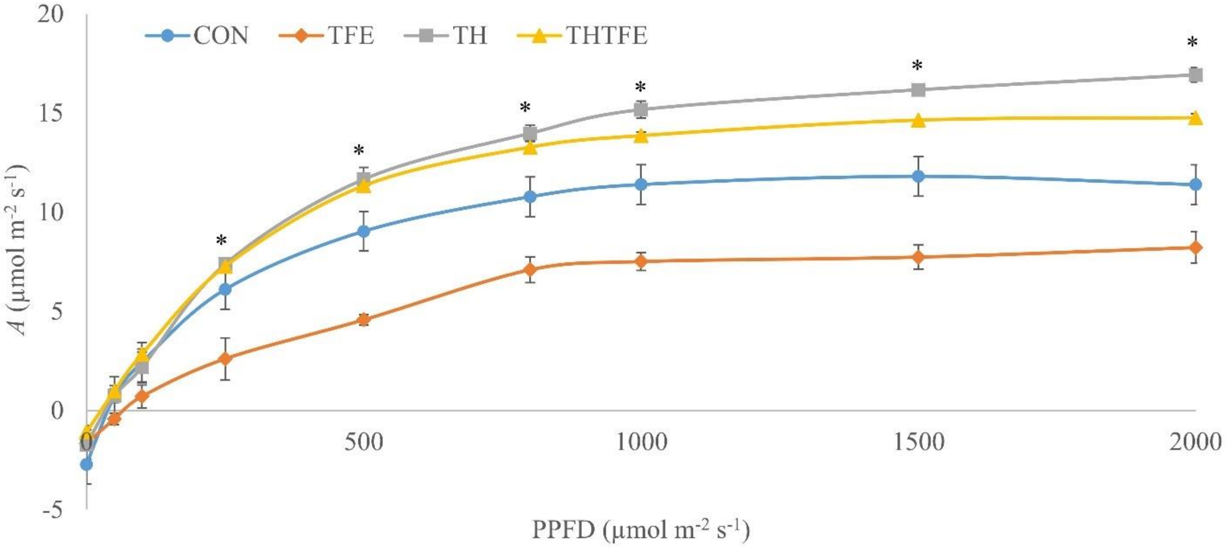

Figure 8. Photosynthetic light response curve across treatments. *A*: net photosynthesis, PPDF: photosynthetically active photon flux density. Values are means and error bars indicate standard error (n=3). Asterisks (*) represents significant differences between treatments (p<0.05). These measurements were taken on the 25th of July in 2016. CON: Control; TFE: Throughfall exclusion; TH: thinning; and THTFE: Combination (Thinning and Throughfall exclusion). Analyzed with two-way ANOVA. *indicates significant differences among treatments (p<0.05).

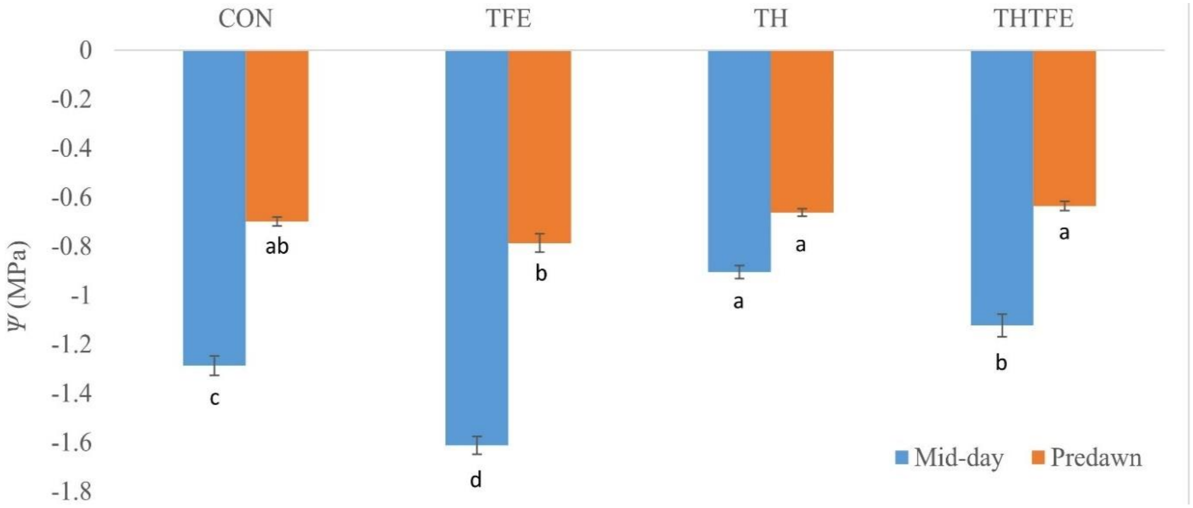

Figure 9. Midday and Predawn plant water potential across four treatments (n=9). Means followed by different letters are significantly different by Tukey's range test (*p*<0.05). These measurements were taken on the 25th of July in 2016. CON: Control; TFE: Throughfall exclusion; TH: thinning; and THTFE: Combination (Thinning and Throughfall exclusion). Analyzed with two-way ANOVA.

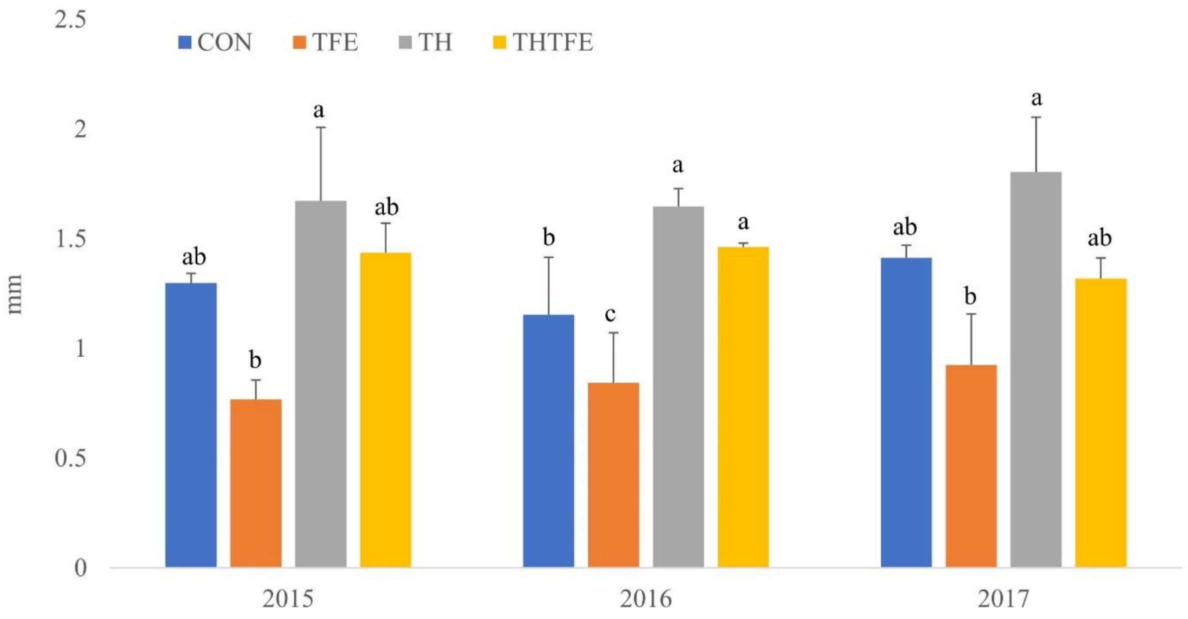

Figure 10. Stem increment across four treatments (n=3). Means followed by different letters are significantly different by Tukey's range test (*p*<0.05). CON: Control; TFE: Throughfall exclusion; TH: thinning; and THTFE: Combination (Thinning and Throughfall exclusion). Analyzed with two-way ANOVA.

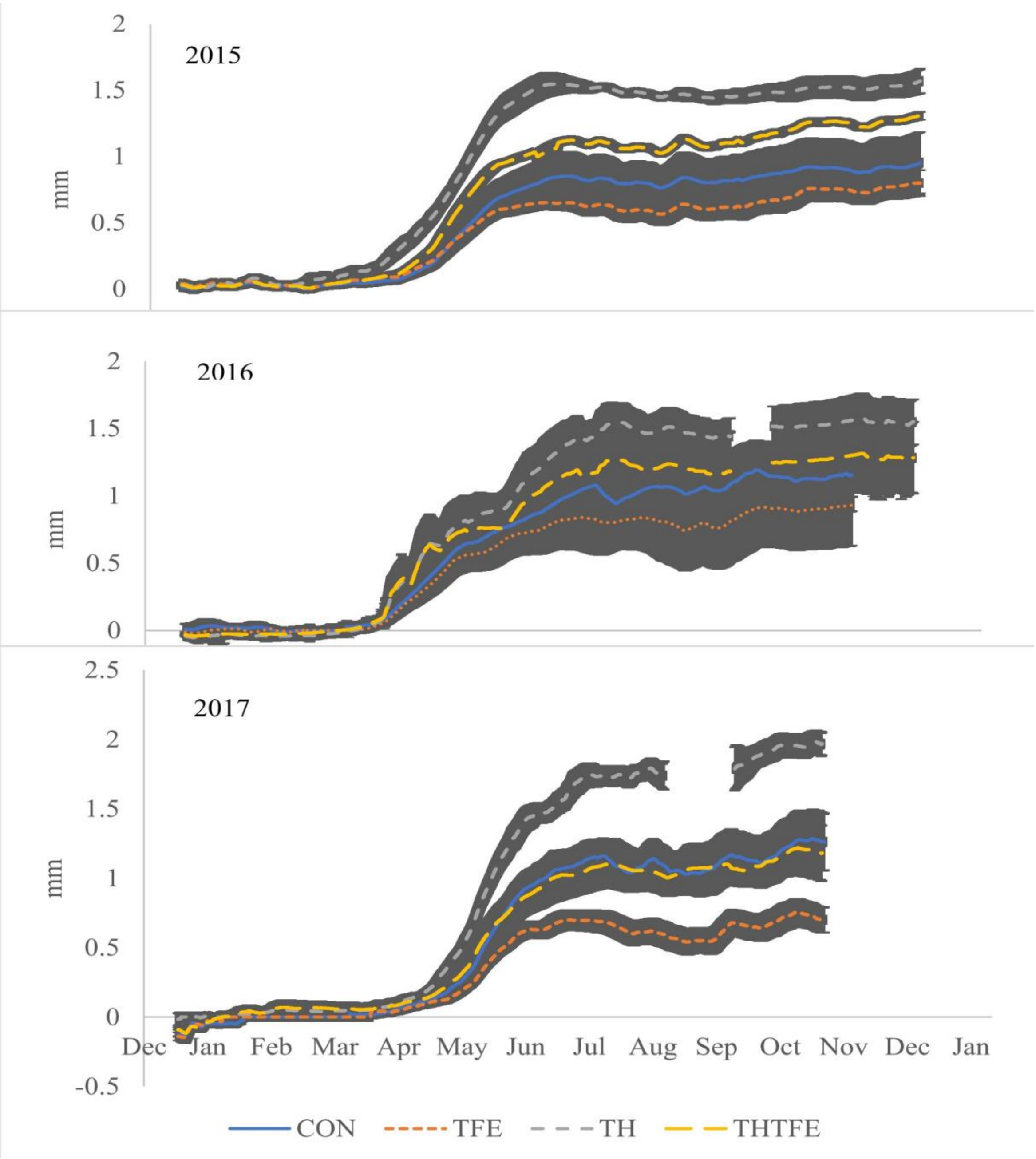

Figure 11. Stem increment fluctuation across four plots from Jan to Dec in 2015. Stem growth started in the middle of March on TH plot, while stem growths on other three plots started on the middle of April (n=3; *p*<0.1) These point dendrometer recoding started on 1st Jan till 31th Dec except year 2017 (Mean ± SE). CON: Control; TFE: Throughfall exclusion; TH: thinning; and THTFE: Combination (Thinning and Throughfall exclusion). Dark grey shading represents SE.

CHAPTER 3

Thinning and Throughfall exclusion affected tree ring $\Delta^{13}C$, WUE$_i$ and basal area increment of a mesic Douglas-fir plantation

Abstract

Climate change will increase air temperature in the Pacific Northwest USA, increasing physiological water stress, which will decrease tree growth. We examined the effects of thinning and a stand-level drought treatment using throughfall exclusion panels on tree growth and physiology to evaluate the drought-mitigating effects of thinning in a rotation-stage Douglas-fir plantation. Thinning significantly enhanced, and throughfall exclusion significantly reduced, soil moisture availability. A regional drought in the summer of 2015, Palmer Drought Severity Index< -3.5, reduced differences in water availability among treatments, and effects persisted into 2016. Standardized basal area increment (BAI) show growth peaking in 1998 (19-year-old stand) shortly after application of a pre-commercial thinning treatment, with relative growth of all pre-treatment plots slowing prior to the experimental setup of thinning and throughfall exclusion treatments in 2014. Thinning significantly increased total BAI, earlywood BAI, and latewood BAI for two years: 80 % BAI increase in 2014 and 45 % increase in 2015 on thinned plots, and a 64 % BAI increase in 2014 and 19 % in 2015 on thinned plots with enhanced drought from throughfall exclusion, in comparison to the control plots. Enhanced carbon isotope discrimination in latewood, and decreased intrinsic water use efficiency (WUE$_i$) in latewood were found on thinned plots for three years. In contrast, the drought treatment did not affect BAI, yet decreased carbon isotope discrimination and increased WUE_i

Keywords: drought, Douglas-fir, thinning, intrinsic water use efficiency, basal area increment, carbon isotopes

Introduction

Increases in frequency and intensity of drought by climate change have been reported (Burke et al. 2006), and these changes are expected to increase tree mortality, and reduce tree growth. A number of studies have already found drought-related, increased tree mortality (Clark 2004; Phillips et al. (Clark 2004; Phillips et al. 2009; Phillips et al. 2010; Peng et al. 2011), forest dieback (Hogg et al. 2002; Breshears et al. 2005; Hogg et al. 2008), reduced net primary productivity and tree growth, (Ciais et al. 2005; Zhao and Running 2010), and decreased seed germination (Braz and de Mattos 2010)

Drought is often considered the single most impactful environmental stress, leading to declines in plant productivity, and increases in physiological stress and mortality (Lambers et al. 2008; Allen et al. 2010). Drought stress results in negative influences on all aspects of plant metabolism; plant growth, physiology, and biochemistry; reductions in biomass accumulation (Liu et al. 2015; Aaltonen et al. 2017), turgor pressure (Huang and Fry 1998), leaf water potential (Samuelson et al. 2014), stomatal conductance, photosynthesis (Warren et al. 2004), sapflow flux and/or transpiration (Pangle et al. 2010) and changes in water use efficiency (WUE, Waghorn et al. 2015). WUE has a critical role in determining plant productivity, an important index measuring a plant's ability to maintain water equilibrium (Gong et al. 2006). Increasing WUE is a strategy to improve crop performance under water limited conditions (Saranga et al. 1999; Araus et al. 2002). WUE is generally defined as the ratio of dry mass accumulated to water loss, the ratio of photosynthesis (A) to transpiration (E) (i.e., instantaneous WUE), and the ratio of photosynthesis (A) to stomatal conductance (g_s) (i.e., intrinsic WUE) (Sinclair et al. 1984). Since instantaneous WUE is measured by gas exchange methods, it represents instantaneous value or responses for short – periods. This method has limitations in describing the long-term physiological responses for environmental changes (Cui et al. 2009) and is unrepresentative of overall carbon and water balance of leaves (Beerling and Woodward 1995). Isotope analysis of tree rings can provide an integrated and annual tree physiological status of intrinsic WUE, thus providing measures of long-term WUE as the isotopes in wood represent the longer-term physiological condition of the plant during photosynthesis. In addition, the stable isotope method is simple and effective in evaluating WUE of plants (Cui et al. 2009).

Thinning as a silvicultural treatment increases wood production through increases in diameter and height, reduces within-stand competition, increases nutrient availability, and accelerates carbon assimilation. Thinning increases water availability to the remaining trees, and stem growth in forest stands, because it reduces stand competition, and improves plant water status (Sucoff and Hong 1974; Bréda et al. 1995; Misson et al. 2003; Moreno and Cubera 2008). The interaction between competition and environmental conditions also influences radial growth of trees within forest stands (Piutti and Cescatti 1997). Crown competition affects not only the space available for growth but also the amount of light that trees receive; root competition for soil water and nutrients also occurs. Thinning results in an increase of soil moisture availability and reduction of plant stress due to a decline in transpiration and rainfall interception losses (White et al. 2009; Park et al. 2018). Light availability also increases with thinning which increases the crown size of of remaining trees (Goudiaby et al. 2011); increasing light as well as nutrient availability (Blanco et al. 2005), leading to an increase in net photosynthesis. Thinning reduces stand-level transpiration, while individual tree level transpiration may increase (Bréda et al. 1995).

Most previous studies on the effects of forest management on tree growth using isotopic analysis have investigated one forest management treatment (e.g., thinning or fertilization), and only a few studies have used a combination of two forest treatments (e.g., Brooks and Mitchell 2011). Artificial drought treatment experiments have been conducted to determine the effects of drought on tree mortality and growth, tree physiology, and soil respiration in the Amazon Rain Forests (Nepstad et al. 2002), Mediterranean forests (Ogaya and Peñuelas 2007; Limousin et al. 2009; Limousin et al. 2010; Misson et al. 2010; Misson et al. 2011), some drought-prone forests in the USA (Hanson et al. 2001; Pangle et al. 2012; Samuelson et al. 2014), and tropical rainforests in China (Zhang et al. 2015). This study is believed to be the first in the mesic productive Douglas-fir plantation system common in the Pacific Northwest, USA. The PNW is expected to have an increase in air temperature with warmer and drier summers over the next century (Mote et al. 2003; Randall et al. 2007; Mote and Salathe 2010). Warmer and drier summers are likely to increase water deficits to forests, and warmer winters will reduce snowpack (Mote 2003).

This study aimed to better understand the effects of thinning and moderate drought on intrinsic water use efficiency (WUE_i) and basal area increment through analysis of tree ring $\Delta^{13}C$. The main objectives of this study were to: 1) determine the impacts of thinning and drought on tree ring $\Delta^{13}C$ and WUE_i; 2) examine the effects of thinning and drought on basal area increment; and 3) evaluate the potential of thinning as mitigation tool against drought events.

Materials and Methods

Site description

The study was conducted in a pure Douglas-fir plantation located in the foothills of the Cascade Mountains (lat. 46°49’18.20”N, long 122°17’33.71”W) at 535-562 m. Douglas-fir and western hemlock were planted in 1979, and precommercially thinned to 300 from 1,250 trees per ha (TPH) in 1993. All western hemlock were removed with precommercial thinning. The stand was 460 trees per ha, 37.1 ± 0.84 cm at 1.37 m height, and 31.49 ± 0.33 m in height prior to treatments. The site is characterized by a Maritime climate, the annual average maximum and minimum temperatures are 15.6 °C and 5.8 °C, respectively, with 100 mm average monthly precipitation, and the driest months of July and August with only a few mm of rain in each month (Gessel et al. 1990).

Experimental Design

A 2 x 2 factorial stand-level treatment was established with two levels of precipitation; ambient and an approximate 40 % reduction (i.e., TFE treatment), and two levels of thinning treatment; none and around 25 % relative basal area reduction. Four plots (40 x 40 m; 0.16 ha) were established, two were thinned, and two were covered with throughfall exclusion structures creating 4 conditions; 1) Control (no thinning and no throughfall exclusion, CON), 2) Throughfall exclusion with no thinning (TFE), 3) Thinning only (TH), and 4) Combination of thinning and throughfall exclusion (THTFE). We established 25 x 25 m core plots on the center of each 0.16 ha plot. Two non-thinned plots had an average of 79 trees, 0.06 ha core plot with 28 trees and the two thinned plots contained an average of 46 trees, 0.06 ha core plot with 13 trees, and a 7.5 m buffer (Table 1). Thinning occurred February to March in 2014, and slash was removed from all plots and piled off-sites. Soil trenches to 60-100 cm depth were created with a ditch-witch, lined with

1m plastic and backfilled with soil to block water flow between plots boundaries in March 2014. Throughfall exclusion installation was completed by the middle of July in 2014. The panels (1.4 x 2.2 m of each panel) were made of wood (Douglas-fir 5 x 5 cm), and tarpaulins installed approximately 1.2 m above ground; the height of panels varied as panels needed to slope and connect to move water off the site. The panels covered approximately 40 % of each plot. The panels prevented rainfall from reaching soils, generating artificial drought on plots. To control for potential warming effects on the two TFE treated sites, tarps with holes were set up on the other two sites (i.e., Control: CON and Thinning: TH) in order to prevent temperature differences among plots; the panels on the CON and TH plots enabled rainfall to reach the soil. Therefore, around 40 % of rainfall reduction occurred on the TFE plot and THTFE plots, compared to the CON and the TH only plots.

Measurements

Environmental monitoring on the site

Site-specific environmental data including air temperature, precipitation and seasonal precipitation (spring, summer, autumn, and winter) for the site from 2011 to 2016 were downloaded using software of Climate WNA with coordinate and elevation of the study site (Wang et al. 2012), and Palmer drought severity index (PDSI) from NOAA (citation) was calculated. Two soil moisture sensors (CD650, Campbell Scientific, Inc) were buried at -20 cm soil depth; one under the panels and another out of panels, and a total five soil water potential sensors (253-L, Campbell Scientific, Inc) were buried at -20 cm soil depth on each plot; three under the panels and two outside the panels, a total of seven soil sensors at -20 cm soil depth were installed on each plot. One soil water potential sensor on each plot was also buried at -60 to 100 cm soil depth.

Sampling

Isotope analysis

Four Douglas-fir trees with similar DBH on each plot (Table 2), had 3 wood cores extracted from 3 directions at 1.37 m height with increment borers: one 5 mm diameter core (reference), and two 12 mm diameter cores. Wood samples were sampled from individual tree rings and for isotopic analysis of the cores for five years (2012 to 2016); two years before treatments, and three years after treatments were conducted.

The reference cores were dried, mounted and sanded on wooden mounts and annual rings were determined to associate rings to specific calendar years in the sample period. All cores were cross-dated and the growth of early and latewood and total year growth were measured using the software, CDendro 7.8. The 12 mm wood samples were dissected into early and latewood under a microscope, and the total wood samples for isotopic analysis were 160 (4 plots x 2 (12 mm) wood cores/tree x 4 trees x 5 years). All wood samples were dried, dissected with razor blades, and ground with a mortar and pestle in preparation for isotope analysis. A total of 120 samples (60 for earlywood and 60 for latewood) were analyzed in the Stable Isotope Core Laboratory of Washington State University, Pullman, WA. We used wood tissue (early and latewood) instead of cellulose because the sample size of the latewood in 2015 was too small to have enough material, and similar $\delta^{13}C$ values between cellulose and wood tissue have been reported in other research (McCarroll & Loader 2004; Sohn et al. 2013, Taylor et al. 2007). Tree-ring wood samples of 0.03 to 0.04 mg were analyzed for Carbon isotopes on an Elemental Analyzer (ECS 4010, Costech Analytical, Valencia, CA). The average analytical precision was 0.05 ‰. All $\delta^{13}C$ values were expressed relative to their respective standard (Vienna Pssdee belemnite: VPDB). Carbon isotope discrimination was calculated with the equation (2) described by Farquhar et al, 1982.

Carbon composition ($\delta^{13}C$) or carbon isotope discrimination ($\triangle^{13}C$) are used to measure intrinsic WUE, and these methods allow an integrative measure of plant responses to environmental stress over longer periods, even though it is an indirect measure (Ferrio et al. 2003). $\delta^{13}C$ was described by Farquhar et al. (1989) and is expressed as:

$\delta^{13}C = [(R_{\text{sample}}/R_{\text{standard})} - 1] \times 1000$ Eq (1);

Where R represents the $^{13}C/^{12}C$ ratio. The $\delta^{13}C$ in the air is in low concentrations, about 8‰, while $\delta^{13}C$ in leaves is around 29‰. The equation for $\triangle^{13}C$ after Farquhar et al. (1989) is:

$\triangle^{13}C_{\text{p}}$ (‰) $= (\delta^{13}C_{\text{a}} - \delta^{13}C_{\text{p}}) / (1 + \delta^{13}C_{\text{p}})$ Eq(2);

Where $\delta^{13}C_a$ and $\delta^{13}C_p$ are air and plant carbon composition, respectively. This equation can be transformed to:

$\triangle^{13}C_{\text{p}}$ (‰) $= a + (b - a)(c_i/c_a)$ Eq(3);

$\delta^{13}C_{\text{p}} = \delta^{13}C_{\text{a}} - a - (b - a)(c_i/c_a)$ Eq(4);

where c_a and c_i refer to ambient and intercellular concentration of CO_2, respectively, a is the discrimination due to diffusion (4.4 ‰), and b is the discrimination due to carboxylation (27 ‰).

Deriving c_i from Eq. 2, the formula reported by Ehleringer and Cerling (1995) were used to calculate intrinsic WUE:

Intrinsic WUE (WUE_i) $= A/g_s = (c_a - c_i)/1.6$ Eq(5);

where 1.6 is the ratio of diffusivities of water and CO_2 in the atmosphere. The carbon isotope discrimination $\triangle$ represents the difference between the carbon isotopic ratio of atmospheric CO_2 ($\delta^{13}C$) and plant organic matter ($\delta^{13}C$), calculated as Eq(2);

‰ was used as $\delta^{13}C$ values, while the values of $\delta^{13}C$ plant were estimated in the rings of our samples. Combining Eq. 2 and Eq. 4, we can derive c_i as:

$c_i = c_a[(\triangle - a)/(b - a)]$ Eq(6);

Inserting c_i from Eq. 6 into Eq. 5, we obtained:

$\mathrm{WUE}_i = (c_a - c_i)/1.6 = [c_a - c_a(\triangle - a/b - a)]1/1.6 = c_a[(1-(\triangle - a / b - a))1/1.6]$;

a and b are known values and c_a is the concentration of CO_2 in the atmosphere; this c_a value was obtained by NOAA (http://www.esrl.noaa.gov/, Mauna Loa station).

Basal area increment estimation

Basal area increments (BAI) for each tree-ring measurement from 1988 to 2016 were calculated using the following formula:

$\mathrm{BAI} = \pi\,(R_n^2 - R_{n-1}^2)$;

where R_n indicates the radius in a particular year and $R_{n\text{-}1}$ the radius of the previous year under the assumption that stem growth approximates the area of a circle (Fritts 2012).

Statistical analyses

The mean of basal increment, $\triangle^{13}C$ and WUE_i were used to test significant differences, and basal increments were normalized by subtracting the mean value of pretreatment years (2011 to 2013) from values for each tree in each year (Brooks and Mitchell 2011). Two-way ANOVA with repeated measures was used to determine significant differences among treatments by years, and Tukey HSD test was used to test for the difference between treatments. All the statistical analyses were performed using R (version 3.2.4), and the R package (dplR version 1.6.6) was used for tree ring width analysis.

Results

Mean air temperature, and precipitation of the site from Jun 2011 to Dec 2016 ranged from 1.5 to 19.7 °C with mean of 10.1 °C, and 1.0 to 320.8 mm with mean of 107.1 mm, respectively. Palmer drought severity index (PDSI), was the lowest (- 3.59) in August 2015. The summer of 2015 had a drought with PDSI below - 3.0, which continued throughout the cool season and into the following summer in 2016, mean of PDSI was - 2.51 (Figure 1). Soil moisture (SM) was significantly different for treatment, month, and year, demonstrating a treatment and seasonality effect. Thinning influenced SM only in 2014 while drought only affected SM in 2015, but treatment effects on SM found in 2016 were restricted to the TFE site (Figure 2-a). More variation in SM in the TH plot was detected than other plots, and SM in the TH plot had the highest values through the research period while SM in TFE had the lowest values. Unlike SM, soil water potential in 2014 and 2016 were affected by drought treatment only. Soil water potential also was the highest on the TH plot while on the TFE plot it was the lowest throughout the measurement period (Figure 2-b). Mean of soil water potential (n=4) at deeper (0.6-1.0 m) soil probes was - 0.19 ± 0.09 MPa, and the lowest was on the TFE plots during the 2015 drought—bottoming at -0.47 MPa in Oct 2015 (Figure 2-c).

The BAI increased from 1988 to 1998 and showed significant differences among four plots from 1989 to 1993 (p<0.05;Figure 3), reflecting differences in initial stocking. However, precommercial thinning (PCT) in 1993 eliminated differences in BAI. The PCT increased the BAI which lasted for 5 years until 1998, after which time BAI began to decline. This decline is expected in fully stocked stands where competition for resources leads to mortality through self-thinning. BAI on both the TH and THTFE plots responded to the second thinning treatment immediately in 2014 (Figure 3). However, BAI across all four treatments decreased in response to drought in 2015 and then increased again in 2016. The TH and THTFE plots showed BAI increase ~80 % and ~64 % respectively in 2014 compared to the CON; BAI increases continued into 2015, although the drought year reduced increases (TH and THTFE with ~45 % and 19 % respectively) compared to the CON plot. Breaking the growth into the earlywood and latewood components through time post-treatment showed: 1) no difference in 2014 earlywood among treatments; 2) 2014 latewood increased 15% more on TH and 35% more on the THTFE plots than the CON; 3) 2015 earlywood BAI increased ~32 % on the TH plot compared to the CON plot; 4) and in 2015 latewood BAI increased ~40 % on TH plot and ~85 % on the THTFE plot compared to the CON plot. Latewood BAI followed the patterns of overall BAI. Increased growth occurred in 2014 and 2015 ($p < 0.05$), but after treatment was applied, only thinning influenced BAI (Table 3). Earlywood BAI on both the TH and THTFE showed significant differences in 2015 compared to the CON. By 2016, the thinning treatment effect on growth was no longer significant. Mean entire BAI (p=0.02 (r=0.82)) and earlywood basal increments (p=0.03 (r=0.80)) across all four treatments were positively correlated with spring precipitation (Mar to May) from 2011 to 2016.

Stable isotope analyses showed similar patterns in response to treatments as the growth data, however they proved to be more sensitive than growth to the treatments, with significant differences between plots both before and after treatments. $\triangle^{13}$C varied from 16.51 to 19.04 ‰ in earlywood and 16.57 to 19.23 ‰ in latewood samples (Figure 4). WUE_i ranged from 86.73 to 116.33 µmol mol^{-1} in earlywood and from 84.66 to 115.66 µmol mol^{-1} in latewood (Figure 5). The relative ranking of $\triangle^{13}$C and WUE_i are similar among treatments in any given, year although in inverse ranking due to the inverse relationship of the metrics. Before treatment applications in 2014 there are significant differences in isotopes among the plots however differences in isotope measurements occurred but did not follow a consistent pattern (Table 4). Variation among plots pretreatment is evidence that sites which were selected to be similar in water availability began with some differences (Tables 4 and 5). The thinning and throughfall exclusion treatments had an overall effect of increasing variation in isotopes and this increased variation was the greatest after thinning in 2014 and 2015, and diminished by 2016.

After the thinning and throughfall exclusion treatment applications, $\triangle^{13}C$ and WUE_i between treatments were significantly different ($p < 0.05$), thinning, drought, and interactive effects were found on $\triangle^{13}C$ and WUE_i on both early and latewood (Table 4, and 5). The treatment effects are apparent in the 2014 latewood samples: the TH treatment shows a decrease in WUE_i and the TFE shows an increase in WUE_i; while the THTFE and CON are similar and of intermediate value. A similar pattern persists in the earlywood samples of 2015. However, the 2015 latewood samples show clear differentiation between the TFE (highest WUE_i) and CON (intermediate value), and the TH and THTFE plots with lower but now indistinguishable WUE_i. In 2016 the WUE_i of all treatments goes down and variation among treatments decreases. The latewood samples show a persistence of the thinning treatment, but a loss of drought treatment effects, as WUE_i of CON is indistinguishable from TFE, and both are greater than TH and THTFE treatments. The impact of thinning on $\triangle^{13}C$ was apparent in the latewood in 2014 and in the earlywood in 2015 compared to other treatments (Figure 4). Also, the effect of drought treatment in latewood $\triangle^{13}C$ on the TFE plot was detected in 2014, but the effect of drought treatment was not significant on the THTFE in 2014. In 2015, the effect of drought treatment on $\triangle^{13}C$ was distinguishable on both early and latewood on the TFE plot and earlywood on the THTFE plot due to combination of drought treatment and severe drought with PDSI of -3.59 (Figure 1). $\triangle^{13}C$ on the TH plot also decreased by ~1 ‰ in 2015 compared to 2014. After the severe drought year, 2015 the $\triangle^{13}C$ overall plots increased in 2016. WUE_i showed opposite trends to $\triangle^{13}C$. WUE_i among four treatments generally increased from 2012 to 2015, then in 2016, all WUE_i decreased. In 2014, WUE_i on the TH plot decreased (Figure 5).

Discussion

BAI and treatments

Our observation that BAI increased immediately after thinning is consistent with previous studies and is why it is a common silvicultural treatment to increase growth of remaining trees (Brooks and Mitchell 2011; Chase et al. 2016; Park et al. 2018). Brooks and Mitchell (2011) showed thinning effects lasted for five years after thinning. Our result showed the first year after thinning BAI increased while in the second year after thinning, a severe drought in 2015 (NOAA) with below - 3 of PDSI, BAI decreased both TH and THTFE (Figure 1). Spring precipitation in 2014 was 476 mm, and 234 mm, less than half the precipitation in 2015. BAI was strongly related to precipitation during the spring, matching Brubaker (1980) showing spring-summer precipitation was positively correlated with tree growth broadly in the PNW including the Olympic, Cascade, Rocky, and Blue mountains.

Far from our expectation, the drought treatment did not reduce BAI significantly when compared to the control. Drought related growth responses depend on species, size class, or age class. Samuelson et al. (2014) found that throughfall exclusion in GA, USA showed no significant differences in either BA or BAI through two years of drought treatment in young loblolly pine. Maggard et al. (2016) also found no significant differences in height growth nor DBH growth between throughfall exclusion and ambient exclusion with loblolly pine in OK, USA. Nepstad et al. (2002) reported that small trees (> 10 cm in DBH and < 15 m in H) were more sensitive to drought treatment than larger trees (> 10 cm in DBH and > 15 m in H), with stem radial growth of small trees reduced by 20 % yet no reduction in radial growth of large trees in an Amazon forest. Barbeta et al. (2013) found the BAIs of *Arbutus Unedo* and *Quercus ilex* reduced by 66.5 % and 17.5 % by drought respectively, but the BAI of *Phillyrea latifolia* was unaffected by the drought in Southern Catalonia, Spain. Other throughfall exclusion studies have shown that the exclusion reduced stem growth compared to control stands (Brando et al. 2008; Rodríguez-Calcerrada et al. 2013). In our study, there are some possible explanations as to why the BAI was not reduced under drought in comparison with the control. First, the thinning effect may be greater than the drought effect (Table 3); an increase in the entire wood BAI on the THTFE combination plot compared to the CON plot supports this explanation. Second, mesic and high productivity plantations with high stocking may lack water limitation — rather light availability limits growth (Case and Peterson 2007; Littell et al. 2010). Third, the drought in 2015 was so extreme that it might have overwhelmed (i.e., increased drought to high levels on all sites) making potential differences between treatments indistinguishable. Fourth, the throughfall exclusion treatment was insufficient to create severe drought on the TFE plot, and/or well-established mature Douglas-fir have low sensitivity to drought; Douglas-fir is well known as drought tolerant and has a heart root system with taproot and extensive lateral roots (Mauer and Palátová 2012). Moreover, the trees on the site were 33-37 years old (2012-2016), mature and > 36 cm in DBH, so they were likely less sensitive to drought treatment. Finally, the soil on the site is relatively deep, and not prone to severe summer drought. The -20 cm soil water potential and deep soil water potentials across all treatments did not go below -0.5 MPa (Figure 2-c). Taiz and Zeiger (2006) suggested that soil water potentials of well-watered garden plants may be as high as -0.5 MPa and typically range from -0.8 to -1.2 MPa. In short, the drought stress, even with TFE was not extreme.

$\triangle^{13}$C *and treatments*

Carbon isotope measures responded to drought more sensitively than tree BAI. We found differences between treatments in 2014, in the year thinning and TFE treatments were applied. Compared to BAI, latewood $\triangle^{13}$C were affected by TFE treatment, resulting in TH>THTFE=CON>TFE. This drought effect lasted into 2015, then disappeared in 2016 after 2 years, suggesting trees made treatment-level adjustments in root biomass and C allocation (Waring and Pitman 1985; Chan et al. 2003). The response of $\triangle^{13}$C on early and latewood on the TH plot in 2014 was different; latewood $\triangle^{13}$C on the TH plot increased after thinning, yet $\triangle^{13}$C of earlywood was not affected by thinning. Some recent research indicates that latewood is synthesized with currently formed photosynthate, whereas earlywood is formed partially using photosynthate assimilated during the previous year (Helle and Schleser 2004; McCarroll and Loader 2004). The increase in latewood $\triangle^{13}$C on the TH plot is probably due to increased g_{s}, by thinning that caused increased soil water availability to the remaining trees, less stand density, and less competition, which leads to less stressed conditions, so that the value of $\triangle^{13}$C fluctuated up and down through three years after thinning. The $\triangle^{13}$C in 2015 decreased due to severe drought, with an increase in $\triangle^{13}$C in 2016. This result is consistent with previous studies of pine species (Warren et al. 2001; McDowell et al. 2003). Warren et al. (2001) found that $\triangle^{13}$C with two pine species increased as Ψ_{soil} increased on both thinned sites (thinned to 250 TPH and 750 TPH), but the relationship was greater in the heavily thinned site. By contrast, sharp decreases in latewood $\triangle^{13}$C on TFE in 2014 and 2015 may have been contributed to by the decrease in Ψ_{soil} by the drought treatment in 2014 and exacerbated by the severe drought in 2015. When the effect of drought treatment on $\triangle^{13}C$ was not significant, the value of $\triangle^{13}C$ increased (Figure 4 and Table 4).

WUE$_i$ and treatments

WUE$_i$ decreased after thinning in 2014, and an increase in g_s (Chapter 1: g_s ranked following TH≥THTFE>CON≥TFE), regulated WUE$_i$ rather than *A* in this study. Both *A* and g_s can be influenced by thinning; previous studies conducted in mesic or wet sites found that *A* was enhanced while g_s was unaffected by thinning, therefore WUE$_i$ was increased or remained stable (Warren et al. 2001; Powers et al. 2009; Brooks and Mitchell 2011), which indicates *A* is a key factor regulating WUE$_i$ in wet sites. In contrast, studies on xeric sites revealed that not only *A* but also g_s were increased by thinning, and the relative increase in g_s was higher than the relative increase in *A*, leading to a decrease in WUE$_i$ (McDowell et al. 2003; McDowell et al. 2006; Moreno-Gutiérrez et al. 2011; Sohn et al. 2014; Giuggiola et al. 2016). Although the study site is mesic, WUE$_i$ decreased unlike previous studies on mesic sites (Warren et al. 2001; Powers et al. 2009; Brooks and Mitchell 2011). It is likely due to size and codominant class of the thinned trees; trees in smaller diameter classes suggest that the *A* of retained dominant trees may not have increased (i.e., prethinned tree's leaves were primarily in high light conditions), or relative increase of g_s (from greater soil water) was higher than that of *A*. Our result supports this theory, we found relative increase of g_s was greater than that of *A* on the site; *A* on the TH and the THTFE plot were around 1.5 x higher (16.9 µmol m^{-2} s^{-1}) and 1.3 x higher (14.7 µmol m^{-2} s^{-1}) compared to the CON (11.3 µmol m^{-2} s^{-1}), respectively, but g_s on the TH plot and the THTFE were 2 x higher (0.26 µmol mol^{-1}) and 1.6 x higher (0.20 µmol mol^{-1}) than on the CON (0.12 µmol mol^{-1}), respectively (Chapter 1). So when comparing WUE$_i$ between CON and TH plots; WUE$_i$ on the TH was lower than on the CON. If the relative increase of *A* was enhanced higher than g_s by thinning, WUE$_i$ on the TH would have been higher than on the CON. However, the value of WUE_i on TH was lower than on CON, which indicates g_s regulated WUE_i more than A on the site. The response of WUE_i to drought treatment was clear and opposite to that of thinning. WUE_i under the thinning treatments might have been regulated by both A and g_s, but increasing WUE_i under drought treatments was ruled out as only driven by decreasing g_s. With comparing WUE_i on the CON with drought treatment, it is obvious that g_s was decreased by the treatment, and this result is in accordance with previous studies that found the g_s decreased as Ψ_predawn decreased (Warren et al. 2001) and average g_s from 56 to 45 mmol m^{-2} s^{-1} was reduced by throughfall exclusion treatment (Samuelson et al. 2014; Samuelson et al. 2017).

Conclusion

Tree growth was positively related to spring precipitation. Thinning successfully enhanced tree growth (BAI) and soil moisture availability, and affected tree physiological responses such as $\triangle^{13}$C and WUE_i. Drought treatment reduced Ψ_soil and influenced $\triangle^{13}$C and WUE_i. Although our drought treatment did not affect tree growth, we could confirm that thinning could mitigate the drought effect on BAI through severe drought in 2015. We speculate that the thinning treatment would mitigate drought effects on tree growth as demonstrated by the combination (i.e., thinning and throughfall exclusion) treatment. Tree growth was not influenced by the mild or weak drought induced by throughfall exclusion, while tree physiological measurements were sensitive to drought. The tree growth on the THTFE plot showed better performance than the TFE plot, and under severe drought year in 2015, the tree growth on the TH plot increased compared to other plots. Therefore, thinning could be a useful drought mitigation tool.

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Tables & Figures

Table 1. Site description before and after thinning treatment . After thinning, around 33 % of stand density (SD) and 25 % of basal area (BA) reduced, respectively. CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively

Plot	CON	TFE	TH	THTFE
Before thinning				
SD (Trees ha^{-1})	475	506	419	419
BA (m^2 ha^{-1})	50.2	54.1	50.8	52.6
DBH (cm)	36.6 ± 0.68	36.5 ± 0.58	38.9 ± 0.9	39.0 ± 0.8
Slope (%)	10~20	10~20	10~20	10~20
Elevation (m)	548	546	548	545
After thinning				
SD (Trees ha^{-1})			275	288
BA (m^2 ha^{-1})			38.2	39.2
DBH (cm)			42.1 ± 0.92	40.8 ± 0.84

Table 2. Diameter at breast height (DBH), and Total height (HT) of four sampled trees in each treatment of Pack Forest at UW (Mean ± SE). CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively

Variable	Treatment			
	CON	TFE	TH	THTFE
DBH (cm)	41.9 ± 0.44 ^{ns}	41.5 ± 0.68 ^{ns}	41.6 ± 0.38 ^{ns}	41.8 ± 0.24 ^{ns}
HT (m)	31.3 ± 1.22 ^{ns}	32.5 ± 2.47 ^{ns}	31.2 ± 0.68 ^{ns}	31.1 ± 0.29 ^{ns}

ns, not significant

Table 3. Summary of significant differences in standardized basal area increments for entire wood, earlywood and latewood after treatment application in 2014. TFE, TH, and THTFE indicate Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively. *indicates significant differences between treatments (*p*<0.05).

	Standardized Basal area increment								
	Entire wood			Earlywood			Latewood		
Treatment	TFE	TH	THTFE	TFE	TH	THTFE	TFE	TH	THTFE
2014	ns	*	ns	ns	ns	ns	ns	*	ns
2015	ns	*	ns	ns	*	*	ns	**	ns
2016	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table 4. Summary of significant differences in $\triangle^{13}$C for earlywood and latewood before and after treatments application in 2014. CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively.

	$\triangle^{13}$C			
	Earlywood			
	CON	TFE	TH	THTFE
2012	17.9 (0.03) ^{c}	18.4 (0.02) ^{b}	19.2 (0.06) ^{a}	18.4 (0.03) ^{b}
2013	18.1(0.02) ^{c}	18.3 (0.02) ^{b}	18.6 (0.01) ^{a}	18.5 (0.02) ^{a}
2014	17.5 (0.00) ^{d}	17.7 (0.01) ^{c}	18.2 (0.01) ^{a}	17.9 (0.01) ^{b}
2015	17.1 (0.00) ^{b}	16.6 (0.02) ^{c}	17.7 (0.03) ^{a}	16.9 (0.06) ^{b}
2016	17.7 (0.00) ^{b}	17.5 (0.02) ^{c}	17.9 (0.08) ^{a}	17.7 (0.02) ^{bc}
	Latewood			
	CON	TFE	TH	THTFE
2012	18.5 (0.06) ^{c}	18.9 (0.04) ^{a}	18.7 (0.02) ^{b}	18.6 (0.02) ^{bc}
2013	18.3 (0.07) ^{ab}	18.3 (0.04) ^{a}	18.4 (0.01) ^{a}	18.1 (0.05) ^{b}
2014	18.1 (0.01) ^{b}	17.5 (0.01) ^{c}	18.8 (0.03) ^{a}	18.2 (0.01) ^{b}
2015	17.2 (0.03) ^{b}	16.5 (0.03) ^{c}	17.7 (0.03) ^{a}	17.7 (0.03) ^{a}
2016	17.4 (0.02) ^{b}	17.5 (0.01) ^{b}	17.8 (0.02) ^{a}	17.7 (0.04) ^{a}

Different letters by treatments (row-wise) indicate significantly different means ($p < 0.05$).

Table 5. Summary of significant differences in WUE_i for earlywood and latewood before and after treatment application in 2014. CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively.

	WUE_i			
	Earlywood			
	CON	TFE	TH	THTFE
2012	98.5 (0.3) ^{a}	93.2 (0.8) ^{b}	85.9 (0.6) ^{c}	93.2 (0.4) ^{b}
2013	97.6 (0.3) ^{a}	94.5 (0.3) ^{b}	91.8 (0.2) ^{c}	92.8 (0.2) ^{c}
2014	104.6 (0.1) ^{a}	102.6 (0.2) ^{b}	97.2 (0.2) ^{d}	100.3 (0.2) ^{c}
2015	110.2 (0.1) ^{b}	115.2 (0.2) ^{a}	103.2 (0.4) ^{c}	111.9 (0.6) ^{b}
2016	103.9 (0.2) ^{b}	106.1 (0.3) ^{a}	101.2 (0.9) ^{c}	104.4 (0.3) ^{ab}
	Latewood			
	CON	TFE	TH	THTFE
2012	93.2 (0.7) ^{a}	87.6 (0.4) ^{c}	89.6 (0.2) ^{bc}	90.6 (0.2) ^{b}
2013	95.1 (0.7) ^{ab}	94.6 (0.4) ^{b}	93.4 (0.1) ^{b}	97.1 (0.5) ^{a}
2014	98.2 (0.1) ^{b}	104.5 (0.2) ^{a}	90.3 (0.4) ^{c}	97.7 (0.1) ^{b}
2015	108.9 (0.4) ^{b}	115.9 (0.3) ^{a}	103.2 (0.3) ^{c}	103.4 (0.3) ^{c}
2016	107.0 (0.3) ^{a}	106.1 (0.1) ^{a}	102.5 (0.2) ^{b}	103.6 (0.4) ^{b}

Different letters by treatments (row-wise) indicate significantly different means ($p < 0.05$).

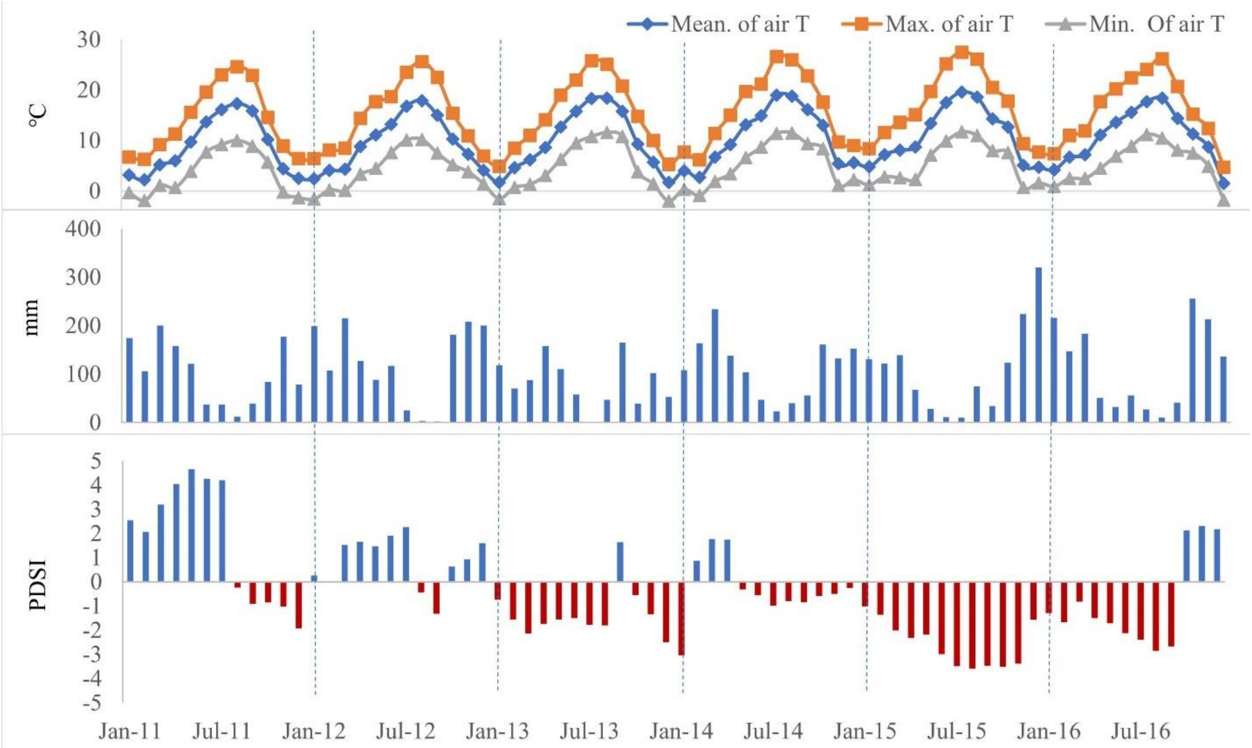

Figure 1. Monthly mean air temperature, precipitation, and palmer drought severity index.

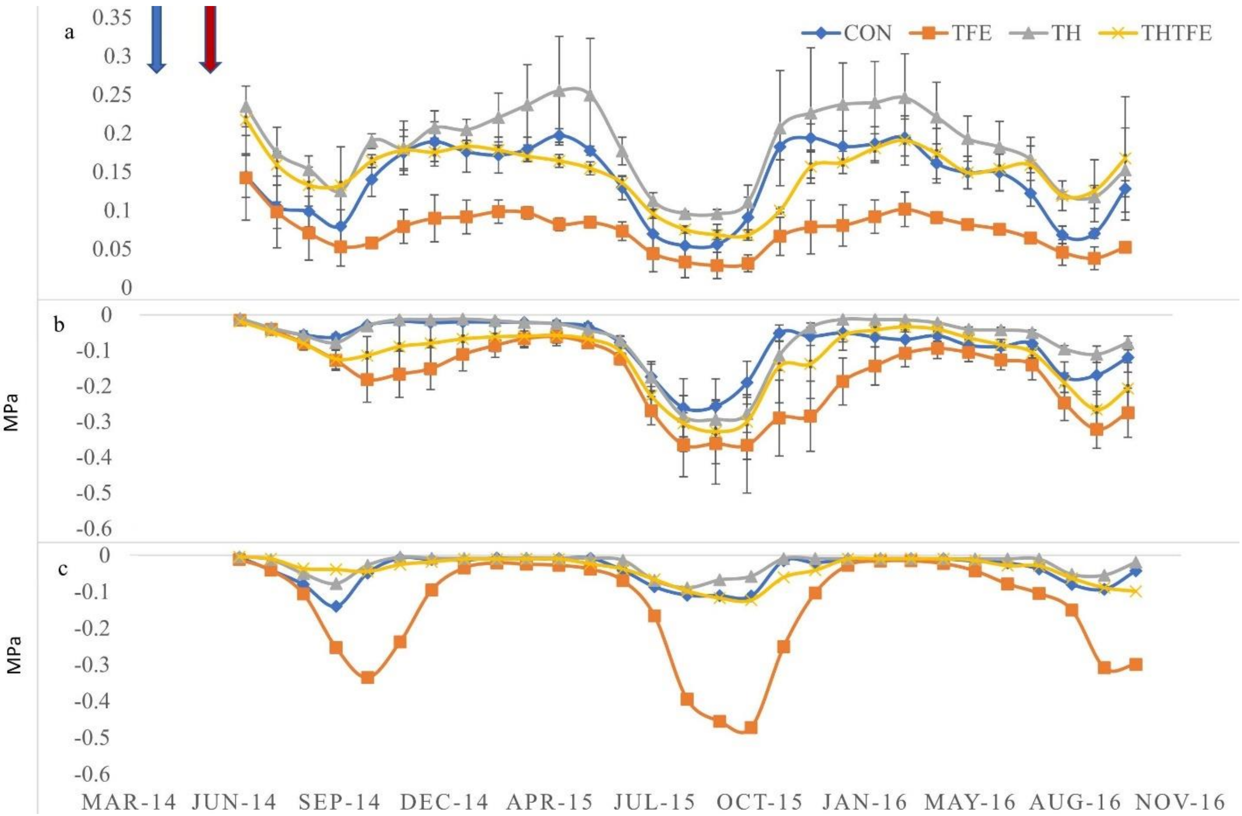

Figure 2. Monthly mean of Soil moisture at -20 cm soil depth (unitless)(a), Soil water potential at -20 cm soil depth (b), and soil water potential at -60 to -100 cm soil depth (c) from Jun in 2014 to Oct in 2016. The first arrow and second arrow (from left) indicate thinning and panel installation, respectively. Throughfall exclusion installation started in March 2014 and completed in July 2014. Thinning completed in February 2014. CON: Control; TFE: Throughfall exclusion; TH: thinning; and THTFE: Combination (Thinning and Throughfall exclusion).

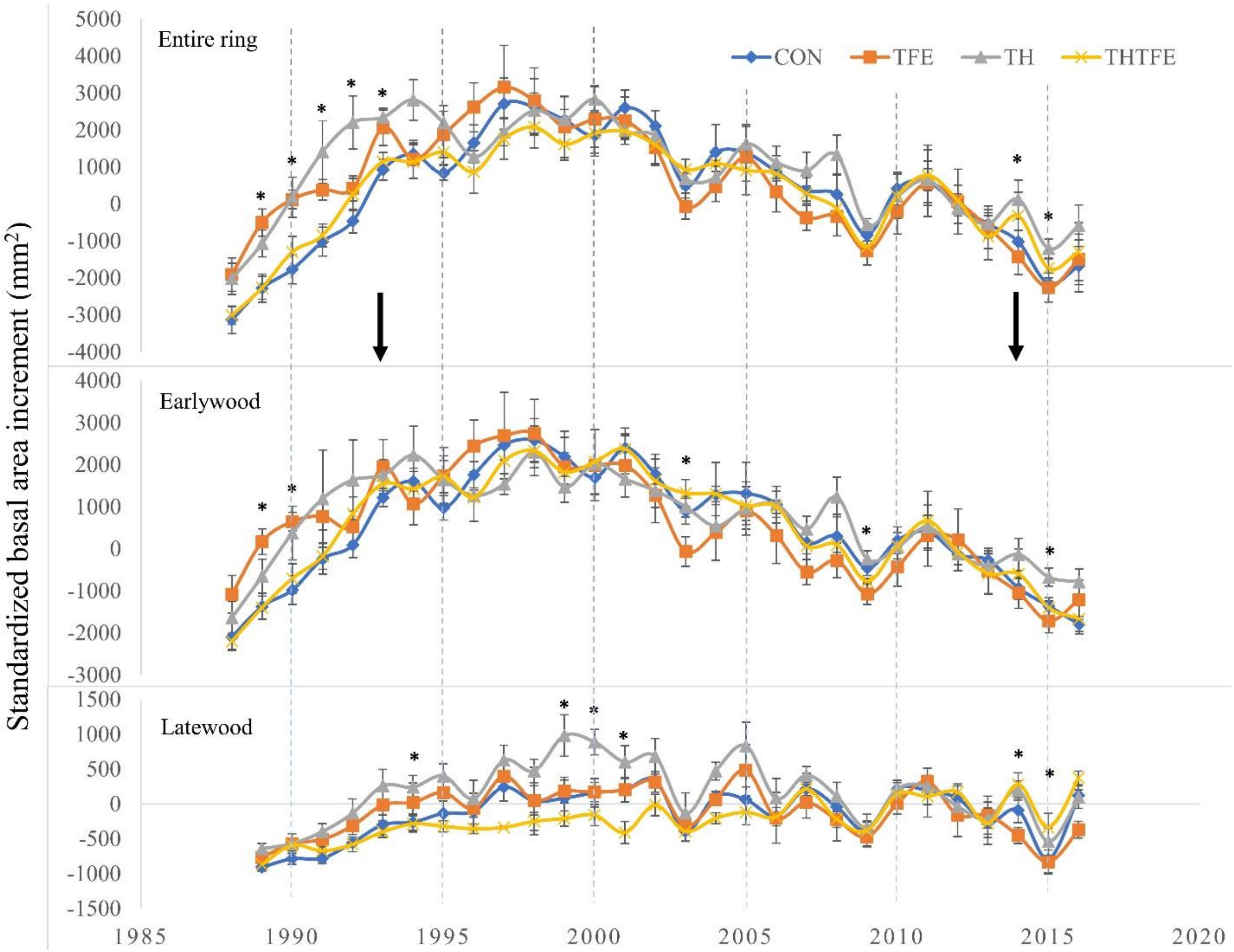

Figure 3. Standardized basal area increment (BAI) (mean ± SE) for the entire ring, earlywood, and latewood. *indicates significant differences between treatments (*p*<0.05). The first arrow from left identifies precommercial thinning and the second arrow when treatments (thinning and throughfall exclusion) were applied to plots. CON, TFE, TH, and THTFE represent control, throughfall exclusion, thinning, and combination (thinning + throughfall exclusion), respectively. Significant differences between treatments are noted in Table 3.

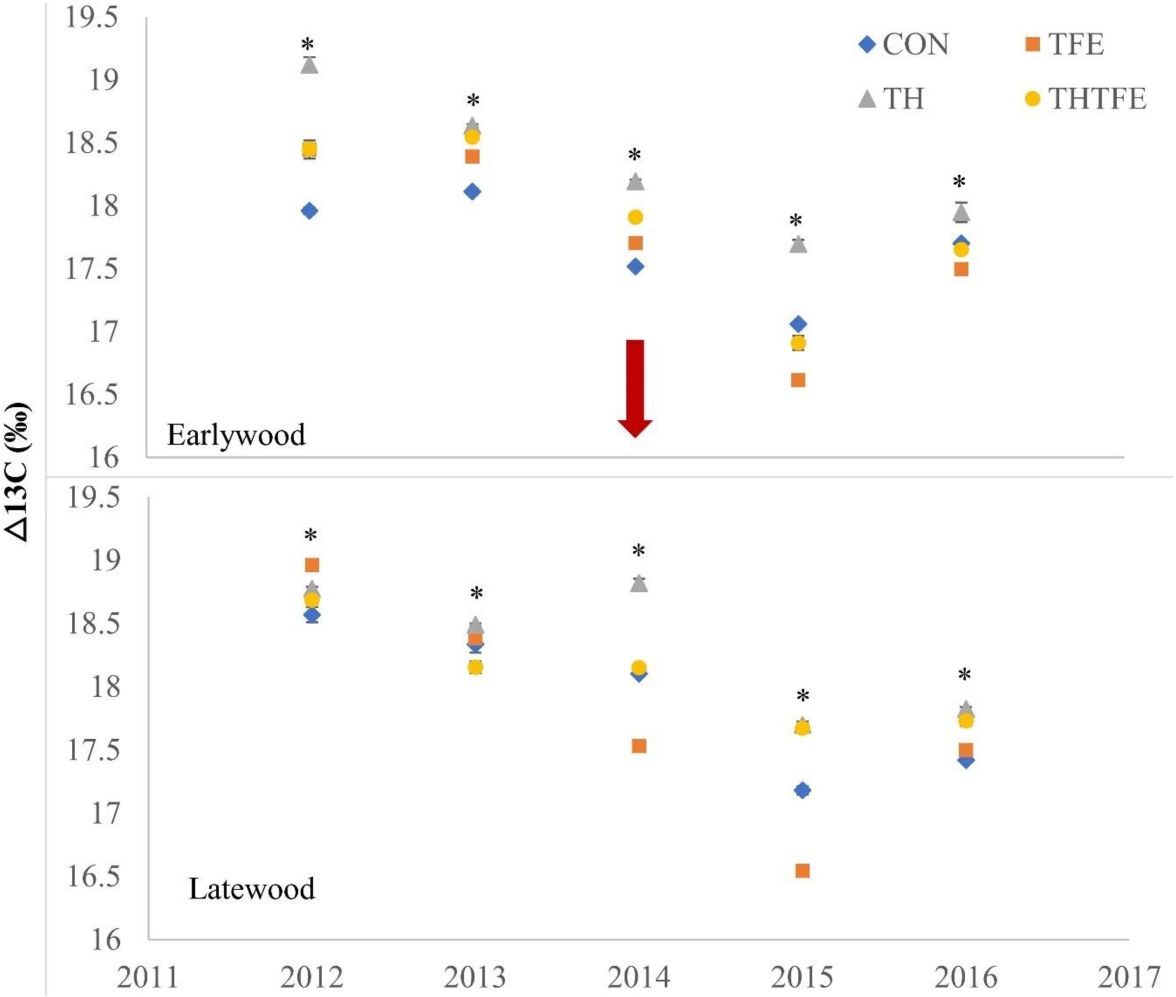

Figure 4. Stable carbon isotope discrimination (mean ± SE) for early and latewood. *indicates significant differences between treatments (*p*<0.05). The arrow indicates treatment application. CON, TFE, TH, and THTFE represent control, throughfall exclusion, thinning, and combination (thinning + throughfall exclusion) respectively.

Figure 5. Intrinsic Water Use Efficiency (WUE$_i$) (mean ± SE) for early and latewood. *indicates significant differences between treatments (p<0.05). The arrow indicates treatment application. CON, TFE, TH, and THTFE represent control, throughfall exclusion, thinning, and combination (thinning + throughfall exclusion), respectively.

CHAPTER 4

Effects of thinning and induced-drought on season soil respiration in a Douglas-Fir plantation

Abstract

Soil respiration is one of the most critical components of the carbon cycle in forest ecosystems emitting 68-77 Pg C y^{-1} globally. Soil respiration is sensitive to climate warming which is predicted to increase temperature and to cause more frequent and severe droughts. To examine the combined impacts of thinning and artificially induced-drought on soil respiration, and soil environmental variables such as volumetric soil water content and soil temperature, a two-way factorial design was conducted (25 % of reduction in stand basal area + 40 % of reduction in precipitation) in a Douglas-fir planation. Soil respiration fluctuated along with seasonal change; during the summer soil respiration increased each month from May to August, and decreased in winter in response to soil temperature at 10 cm soil depth. Soil respiration peaked in August and bottomed in December. Drought treatments lowered soil respiration by ~34 % compared with the control plot. Soil respiration on the thinned plot and in the combination plot (thinning and drought) were not significantly different from the control plot. Two treatments influenced VWC: thinning increased VWC by ~230 % in comparison with control, while drought reduced it by approximately 50 % compared to control. Soil temperature between treatments was not significantly different. Soil respiration was positively related to soil temperature among the four treatments, but negatively correlated to volumetric soil water contents on the thinning and combination plot. Q_{10}

was reduced only by drought ($p<0.05$). The results suggest that drought (throughfall exclusion of precipitation) results in significant decreased in *Rs* from soils, but the decrease in *Rs* are likely compensated for by thinning.

Keywords: throughfall exclusion, thinning, drought stress, soil respiration, *Pseudotsuga menziesii*

Introduction

Soil respiration (R_s) is one of the most critical components of the carbon cycle in forest ecosystems (Jassal et al. 2008). Soil respiration contributes 60-90% of all respiration in the global carbon cycle (Hanson et al. 2000), and it is less well understood than other components of the carbon cycle (Striegl and Wickland 1998). Soil respiration is around 68 -77 Pg C/yr, ten times more than anthropogenic carbon emission (Raich and Schlesinger 1992; Raich and Potter 1995; Raich et al. 2002). A better understanding of *Rs* is critical to carbon mitigation strategies (Raich et al. 2002; Xu 2006).

R_s is defined as the production of CO_2 from soils when soil organisms and roots respire during their metabolic activities (Luo and Zhou 2006). R_s is mainly composed of autotrophic respiration (R_a) from plant roots and their symbionts and heterotrophic respiration (R_h) from litter and soil organic carbon decomposition (Hanson et al. 2000). R_s is affected by environmental factors such as soil temperature, soil water content (VWC), and nutrients in soils (Luo and Zhou 2006). Previous work reported that increasing soil temperature stimulates R_s (Fang and Moncrieff 2001; Drewitt et al. 2002; Yuste et al. 2003; Jassal et al. 2008), and Schimel et al. (2001) used experimental warming treatments to demonstrate that increasing temperature increased soil respiration. Lu et al. (2013) detected that R_s increased by 9-20 % under experimental warming treatments. R_s and R_a under elevated CO_2 also increased (Zak et al. 2000; Nie et al. 2013). Increased temperatures in humid environments are likely to stimulate microbial activity so that R_s increases, while in dry soils increased temperatures may result in drier conditions, leading to a negative R_s response to temperature (Ciais et al. 2005; Wan et al. 2007). Yet, responses of soil emission to precipitation are variable, and ecosystem–dependent, which suggests that soil respiration responses to soil moisture are also variable (Borken et al. 2006; Tang et al. 2006). Generally, drought is more likely to reduce soil respiration (Chang et al. 2016; Hoover et al. 2016; Liu et al. 2018) due to soil environmental conditions, and lower soil microbial activities (Skopp et al. 1990).

Forest management such as thinning, clear-cut harvesting, and burning can influence soil respiration. Clear-cut harvesting reduced soil respiration compared to undisturbed Jack pine forests due to destruction of soil R_a and R_s on the soil surface and death of tree roots on the harvested site (Striegl and Wickland 1998). In contrast summer soil respiration increased in harvested sites dominated by western hemlock, Douglas-fir, and western redcedar (Marra and Edmonds 1996). Yet, long-term research (15 years) with harvest residue management (slash burning, whole-tree harvest, stem only harvest, and double residue) on sites replanted with Chinese fir (*Cunninghamia lanceolate* (Lamb.) Hook) showed no differences in soil respiration (Hu et al. 2014).

Thinning modifies forest environmental conditions by reducing stand density and increasing canopy openness, soil water availability, and soil temperature, effecting R_s (Ma, Chen et al. 2004). Thinning causes root death of removed trees, which, in turn, lowers R_a. However, short-term increases in R_s are expected due to the decay of litter, fine and coarse woody debris (including roots) (Ohashi et al. 2000; Son et al. 2004; Sullivan et al. 2008). Ohashi et al. (1999) revealed that R_s was higher in thinned stands than in control stands within the first four years after thinning; however, no significant differences were observed after five years. Ma et al. (2004) found a significant difference between thinned and control plots only in the first year after treatment, and in some cases thinning had no significant effect on *Rs* (Campbell et al. 2009).

In the PNW, R_s was positively related to soil temperature and was negatively affected by soil water stress when soil water potential was -2 MPa in 18 year-old Douglas-fir stands (Jassal et al. 2008). However, no significant effects of VWC on R_s on study sites dominated by Douglas-fir were found in the Olympic National Park (Kane et al. 2003), although VWC was relatively high (16-30%). Jassal et al. (2010) found that the addition of N increased soil respiration over 3 to 4 months due to an increase in R_a. Mostly R_s studies in PNW have focused on seasonal changes, and only a few studies were conducted with forest applications such as thinning or burning. So the study of R_s with artificially induced-drought treatment and thinning provides needed information which may be crucial in understanding the potential mitigating effects of lower intensity harvest practices such as thinning on forest carbon cycling.

The objectives of this study were to determine the effects of drought (reduced soil moisture) and thinning on R_s in maturing Douglas-fir (35 years) plantations. We measured seasonal variation in soil respiration to evaluate the influence treatments had on the relationship between soil respiration and soil temperature and soil volumetric water content.

Materials and Methods

Site description and experimental design

Soil respiration (R_s) field measurements were taken in two uniformly spaced, fully stocked Douglas-fir plantations (27 year-old and 10 years older) throughout the year, to compare changes on thinned and unthinned sites. A two-factorial design was used for the supplementary study site with the 27-year-old Douglas-fir stand. The design allows a replicated measurement of soil respiration under: 1) closed canopy, fully stocked plantation, 2) thinned areas within the same stands. Also, in order to determine the immediate effect of TFE (throughfall exclusion), one more plot with CON (control) and TFE treatments was set up on the Canyon loop firewood stand to determine the immediate responses to drought treatment. This plot was ~20 m away from the TFE study site (the details on these supplementary studies are described in Appendix 1).

Measurements

R_s measurement

In each plot, 5 PVC soil collars (98 cm^2 in area and 5 cm in height) were permanently installed 3 cm into the soil in September 2014, avoiding tree stumps, boulders, and big roots. The distance between adjacent collars was more than 1 m. Soil respiration was measured 1-2 times per month from November 2014 to October 2015 using a Li-6400 infrared gas analyzer (Li-COR, Inc., Lincoln, Nebraska, USA) connected to a Li-6400-09 soil respiration chamber (9.55 cm diameter) (Li-COR, Inc., Lincoln, Nebraska, USA). Measurements were taken between 10:00 am and 3:00 pm. Soil temperature at 10 cm below the soil surface was also monitored with a thermocouple sensor attached to the respiration chamber during the R_s measurement. Volumetric water soil moisture (VWC) of the top 10 cm soil layer was measured near each soil respiration collar using a Hydrosense II (HSII, Campbell Scientific, Inc) concurrently with the soil respiration measurements. When VWC value was 0 % at first measurement, VWC was measured again, and the second measurement was used unless the second measurement value was also 0 %. The measurement methods were also applied to the two additional R_s measurement sites.

Q_{10} calculation

Q_{10} was calculated to describe the sensitivity of soil respiration to temperature. Q_{10} is a temperature coefficient of the ratio of respiration rates over a 10°C soil temperature interval. For each treatment, a Q_{10} value for the measurement period (Nov 20014 to Oct 2015) was computed from monthly measurements of R_s and soil temperature following equations of Lloyd and Taylor (1994), where:

$R_s = \alpha e^{\beta T}$ (1), and

$Q_{10} = e^{10\beta}$ (2);

and where R_s is measured soil CO_2 efflux, T is measured soil temperature at a depth of 10 cm, and α and β are regression coefficients.

Statistical analysis

Monthly means of soil respiration rate, soil moisture, and soil temperature by treatments were calculated as the means of five collar measurements. Repeated measure Analysis of Variance (ANOVA) was used to test the differences in soil respiration rate, soil temperature, and soil moisture among treatments. Tukey multiple comparisons of means were used to compare the differences of each variable. Pearson correlation coefficients were used to compare the relationship between soil respiration and environmental variables. The R_s models were compared to determine the differences between treatments. All of the tests were performed using R (version, 3.4.4)

Results

The mean annual R_s was significantly lower for the TFE treatment (1.83 ± 0.17 µmol m^{-2} s^{-1}) than all other treatments: the THTFE (2.60 ± 0.32 µmol m^{-2} s^{-1}) and the CON (2.76 ± 0.49 µmol m^{-2} s^{-1}) treatments were similar but significantly lower than the TH site respiration (2.89 ± 0.41 µmol m^{-2} s^{-1};Table 1). R_s in the CON, TH, TFE, and THTFE plots ranged from 0.87 to 5.4 µmol m^{-2} s^{-1}, 0.83 to 2.74 µmol m^{-2} s^{-1}, 1.08 to 5.17 µmol m^{-2} s^{-1}, and 1.44 to 4.75 µmol m^{-2} s^{-1}, respectively. The overall effect of differences in temperature and panel-induced drought was best captured by Q_{10} which was almost twice as high on the fully stocked non-drought site (i.e., control) as all other treatments; unthinned, and drought-enhanced stands had notably lower respiration (Table 4;Figure 6).

Seasonal pattern in R_s, VWC, and ST to treatments

R_s varied considerably by season with winters showing the lowest overall respiration (a temperature limitation) with similar responses by treatment. Summer R_s was responsive to drought treatments and thinning showed significant differences (p<0.05; Figure 3-c)—highest respiration was on the two sites (control and thinned) where drought-enhancement was not present (Figures 3-c). R_s increased by season changing from winter to summer, and summer R_s was around twice that measured in winter. ST and VWC also varied with season, with the lowest temperature and highest soil moisture during winter. R_s peaked in August and was at a low-level November-February. ST followed an expected temperate pattern and was positively correlated with R_s (Table 2; Figure 4). VWC was more variable among treatments than ST, ranging from 2.26 to 30.62 % across four plots. VWC in summer was not different among treatments except VWC on the TH plot, but in winter VWC on the CON was significantly different from TFE and THTFE plots. VWC on the TH plot was the highest among treatments during the research years (p<0.05; Figures 3-b). VWC in CON, TH, TFE, and THTFE plots ranged from 2.26 to 19.7 %, 2.28 to 7.9 %, 11.52 to 30.62 %, and 0.14 to 11.18 %, respectively (Figure 3-b).

The relationship between Rs and ST, and VWC

R_s was positively correlated with soil temperature across four treatments and correlated to volumetric soil water content only on the CON and TH plots. R_s responded to temperature similarly in both thinned sites (with and without throughfall exclusion), however on the unthinned sites (TFE), the increase in R_s with increasing temperature was slower (Table 3; Figure 4). On the contrary, R_s showed no significant response to soil water content on the drought-enhanced sites

(Table 3; Figure 5). The relationship between R_s and VWC across four treatments was generally negative, yet the relationship on TFE plot only showed a positive trend although it was not significant. R_s was negatively correlated with VWC only on the non-TFE sites (Figure 4); throughfall exclusion lowered VWC sufficiently that R_s was unresponsive to changes in VWC on these plots (i.e., it was too dry).

Discussion

The estimated value of global R_s ranges from 75 to 98 Pg Cyr^{-1}, which is more than ten times the amount of fossil fuel combustion (Raich et al. 2002; Bond-Lamberty and Thomson 2010), and global mean Q_{10} was 2.4, ranging from 1.3 to 3.3 (Schlesinger and Andrews 2000; Qi et al. 2002). Jassal et al. (2008) found that summer R_s in a 17-year-old Douglas-fir plantation on Vancouver Island, Canada, peaked at ~10 μmol m^{-2} s^{-1}, ranging from ~2 to 10 μmol m^{-2} s^{-1}, and Q_{10} ranged from 1.49 to 4.25. In this study, Q_{10} across four plots ranged from 2.55 to 6.32. These values were higher than average value of 2.4 (between 1.3 to 3.3) from other studies (Schlesinger and Andrews 2000; Qi et al. 2002), and a meta-analysis reported that mean Q_{10} value from 0 ℃ to 20 ℃ was 3.0 ± 1.1 (Bond-Lamberty and Thomson 2010), which indicates that the study site is sensitive to change in soil temperature. R_s varied with the season; the average R_s was highest in summer followed by R_s in spring, R_s in fall, and R_s n winter. R_s in summer was higher than other seasons, which is related to the increase in soil temperature, and growing season of understory plants on the sites such as salal (*Gaultheria shallon* Pursh), and swordfern (*Polystichum minutum* Kaulf.). For example, root respiration generally relies on the amount of photosynthates translocated from the aboveground part of the trees (HoÈgberg et al. 2001). Therefore, root respiration is prone to be sensitive to seasonal change in photosynthetic activity (Curiel Yuste et al. 2004) such that R_s in growing seasons, spring and summer, are higher than in other seasons. Previous studies found that drought and fertilization applications affected the soil Q_{10}. The result of Q_{10} reduction on drought plots in this study is consistent with others (Jassal et al. 2008; Chang et al. 2016). The reduction of Q_{10} is likely due to decreases in VWC; water stress leads to an increase in diffusion resistance, decrease substrate supply, and reduces the contact between substrate and the extracellular enzymes and microbes involved in decomposition (Davidson et al. 2006; Jassal et al. 2008).

Responses of ST and VWC to treatments

We expected that the two treatments would alter the patterns of environmental variables such as ST and VWC. VWC observed in the study indicated that the treatments altered the patterns of VWC through changing canopy structure by thinning, and by the positioning of panels and gutters (Pangle et al. 2012). We also expected that the TFE treatment might have created some shade so that ST under treatment would decrease, yet, that effect was not found in the study. ST observed in the study suggested that the thinning had partial or no impact on soil temperature. Previous studies have already noted that thinning affects site-specific microclimate conditions (Masyagina et al. 2010; Wang et al. 2013), and ST increase by the removal of aboveground vegetation (Köster et al. 2011).

Rs responses to drought treatment

Throughfall exclusion treatment decreased R_s over the research period (Figure 3-c). The reduction in R_s on drought plots was observed in other precipitation manipulation studies as well (Borken et al. 2006; Chang et al. 2016; Hoover et al. 2016; Liu et al. 2018). Throughfall exclusion decreases VWC, lowering soil moisture contents directly affects the production and breakdown of the organic matter forming the substrate for R_h (Linn and Doran 1984), and induced an environmental condition slowing the diffusion of solutes, therefore microbial respiration is depressed by limiting the supply of substrate (Skopp et al. 1990). Also, this altering VWC influences physiological processes of roots and micro-organisms (Williams and Rice 2007). Several drought studies found that C allocation which is recently assimilated to roots decreases under drought stress (HoÈgberg et al. 2001) so that the growth and respiration of roots and microbes reduce because they put more energy to produce protective molecules (Schimel et al. 2007). Moreover, Atkin and Macherel (2008) suggested the reduction in R_s under drought stress is related to a decline in root growth, impaired root cell integrity and limited supply of substrate. The results of the study detected the positive relationship between *Rs* and VWC under drought treatment, although it was not significant, it provides evidence that reduced soil moisture depresses R_s .

Interestingly, some studies found that reduced soil moisture did not lower R_s (Lu and Zhang 1998; Liu et al. 2004; Asensio et al. 2007; Chang et al. 2016). Two Oak species showed different responses of *Rs* to drought treatments in the first year of a drought study. R_s of *Quercus ilex* increased under drought treatment while that of *Q cerrioides* decreased due to differences in root systems (Chang et al. 2016), and Liu et al. (2004) explained increase in R_s under drought condition resulted from root:shoot ratio changes and enhanced photosynthesis rate by moderate drought (Lu and Zhang 1998).

Rs responses to thinning

Previous studies of the effect of thinning to R_s varied; R_s after thinning remained unchanged (Ohashi et al. 2000; Carter et al. 2002; Masyagina et al. 2010), increased or seasonally increased (Londo et al. 1999; Ma et al. 2004; Pang et al. 2013), and decreased (Tang et al. 2005; Jónsson and Sigurðsson 2010). Chang et al. (2016) mentioned that these different responses probably resulted from thinning intensity, timing, and period of measuring R_s after thinning.

In our study, neither an increase nor decrease in R_s after thinning was found. R_s after thinning might have been decreased due to the reduction in tree root respiration, and this assumption is consistent with the result of previous studies. Pang et al. (2013) found the reduction in R_s after thinning during the first spring (February to April), and Tang et al. (2005) described that this decrease in R_s was attributed to a decline in root respiration due to loss of root biomass and reduction in photosynthesis after the removal of the tree crown during the thinning (Tang et al. 2005; Pang et al. 2013). However, our results showed no difference in R_s between control and thinned plots seven months after thinning. It is assumed that the decomposition of dead roots likely contributed to an increase in R_s on thinned plots (Wang and Yang 2007; Chen et al. 2010).

Moreover, we found that the understory vegetation cover and abundance on thinned plots were significantly higher than in other plots, so that root respiration from understory vegetation could offset the reduction in R_s from tree root respiration on thinned plots (Pang et al. 2013). Pang et al. (2013) also stated that increases in root respiration and photosynthesis from new understory vegetation possibly compensate for the reduction of R_s after thinning. Previous studies revealed that light use efficiency on thinned plots increased by 60 % compared with that on unthinned plots, and this increase in light use efficiency was likely attributed to increasing fine root production and shrub production (Campbell et al. 2009; Gauthier and Jacobs 2009).

Conclusion

In conclusion, we determined the effects of thinning and drought on R_s, VWC, and ST in a Douglas-fir plantation, and found a significant change in R_s and VWC due to throughfall exclusion induced drought. The drought significantly depressed R_s and VWC; R_s under drought reduced by 34 %. Thinning did not change R_s significantly, yet increased VWC. Thinning therefore mitigated the negative effect of drought on R_s. We also observed that drought treatment reduced Q_{10} of R_s.

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Tables & Figures

Table 1. The annual mean of Soil respiration (*R_s*), Soil temperature (ST), and Volumetric water content (VWC) along with treatments. CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively

	CON	TFE	TH	THTFE
Rs (μmol CO_2 m^{-2} s^{-1})	2.76 (0.49) ^{a}	1.83 (0.17) ^{b}	2.89 (0.41) ^{a}	2.60 (0.32) ^{ab}
ST (°C)	9.94 (1.03) ^{ns}	9.88 (0.99) ^{ns}	10.26 (1.04) ^{ns}	9.92 (0.94) ^{ns}
VWC (%)	9.49 (1.78) ^{b}	4.93 (0.66) ^{c}	23.99 (2.16) ^{a}	5.65 (1.30) ^{c}

Lowercase letters indicate significantly difference ($p < 0.05$) ns; not significant

Table 2. Statistical significance for the effects of Month, Throughfall exclusion (PA), and Thinning (TH) on Soil respiration (R_s), Soil temperature (ST), and Volumetric water contents (VWC) at depth of 10 cm from Nov in 2014 to Oct in 2015. * *p*<0.001; ** *p*<0.01; * *p*<0.05.**

Plot	R_s	ST	VWC
TH	<0.001 ***	<0.01 **	<0.001 ***
PA	<0.001 ***	<0.01 **	<0.001 ***
Month	<0.001 ***	<0.001 ***	<0.001 ***
TH:PA	<0.05 *	0.634	<0.001 ***
TH:Month	0.948	<0.001 ***	<0.001 ***
PA:Month	<0.001 ***	<0.001 ***	<0.001 ***
TH:PA:Month	0.421	0.426	<0.001 ***

Table 3. Correlation coefficient of Soil respiration (*Rs*) with Soil temperature (ST) and Volumetric water contents (VWC). CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively. * *p*<0.001; ** *p*<0.01; * *p*<0.05.**

	PLOT	ST	VWC
R_S	CON	0.88 ***	-0.70 *
	TFE	0.93 ***	0.16
	TH	0.84 ***	-0.87 ***
	THTFE	0.92 ***	- 0.41

Table 9. Coefficient constants for the exponential model and *Q_{10}* of each plot during the research year. CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively.

	α	β	R^2	Q_{10}
Total	0.65	0.13	0.65	3.76
CON	0.38	0.18	0.79	6.32
TFE	0.68	0.09	0.82	2.55
TH	0.83	0.12	0.63	3.23
THTFE	0.71	0.12	0.88	3.49

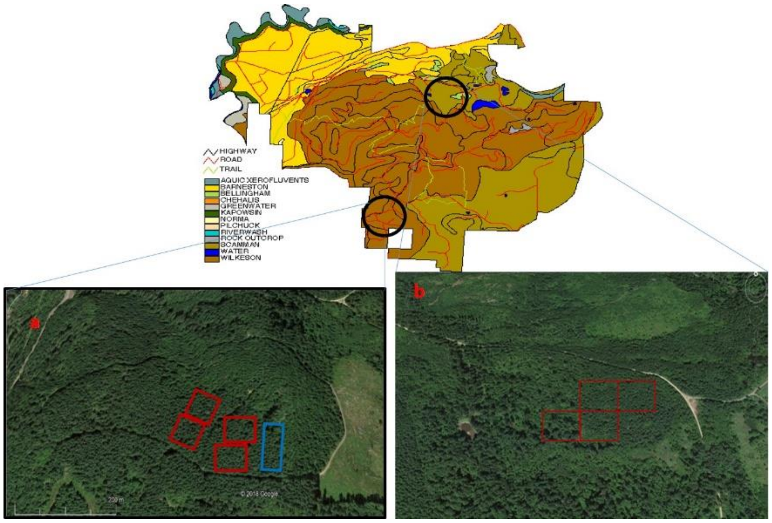

Figure 1. Soil respiration study sites on Canyon Loop Firewood stand (a) and Clear cut stand (supplementary) (b). Red boxes on figure a indicate original R_S study, and a blue box indicates additional R_S study spot.

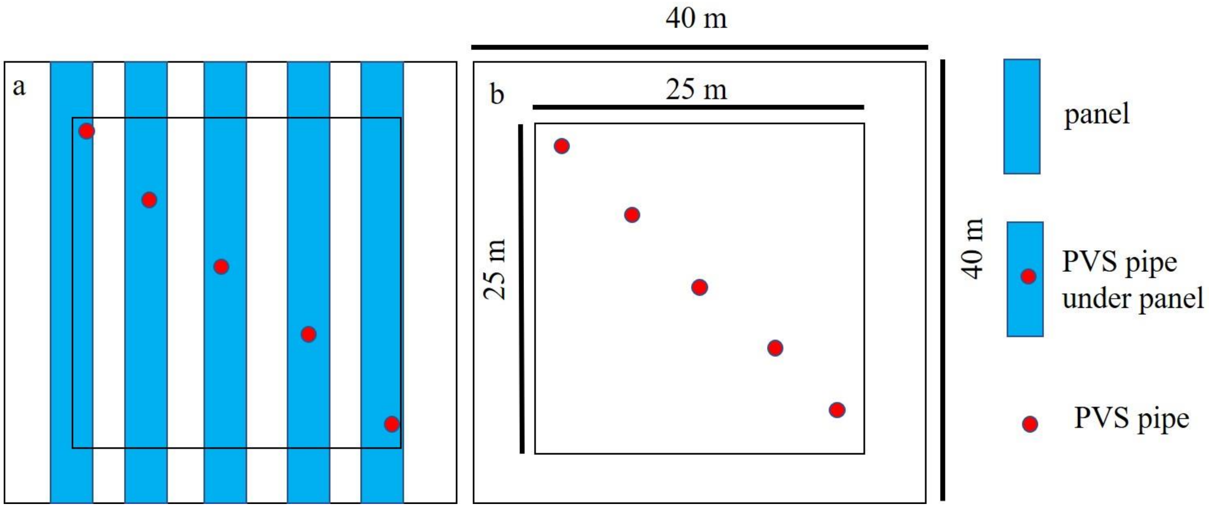

Figure 2. Field plot layout (40 x 40 m). a) Five soil respiration collars under panels on TFE and THTFE plots inside the core plot (25 x 25 m). b) Five soil respiration collars were set up out of panels on CON and TH plots.

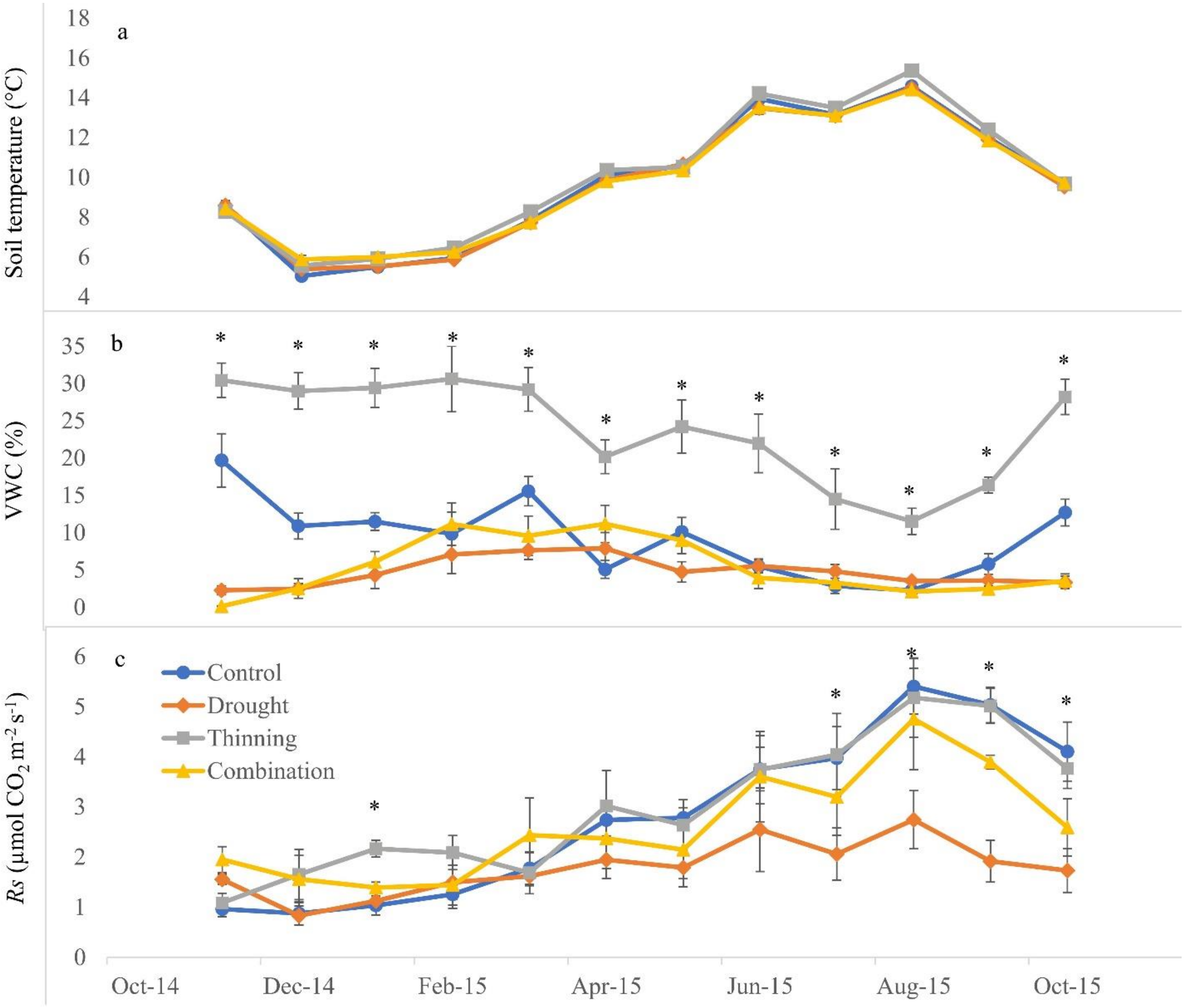

Figure 3. Seasonal variations of soil temperature (ST)(a) at -10 cm depth, volumetric water content (VWC)(b) at -10 cm depth, and soil respiration (*R_s*)(c) from Nov in 2014 to Oct in 2015. CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively. *indicates significant differences between treatments.

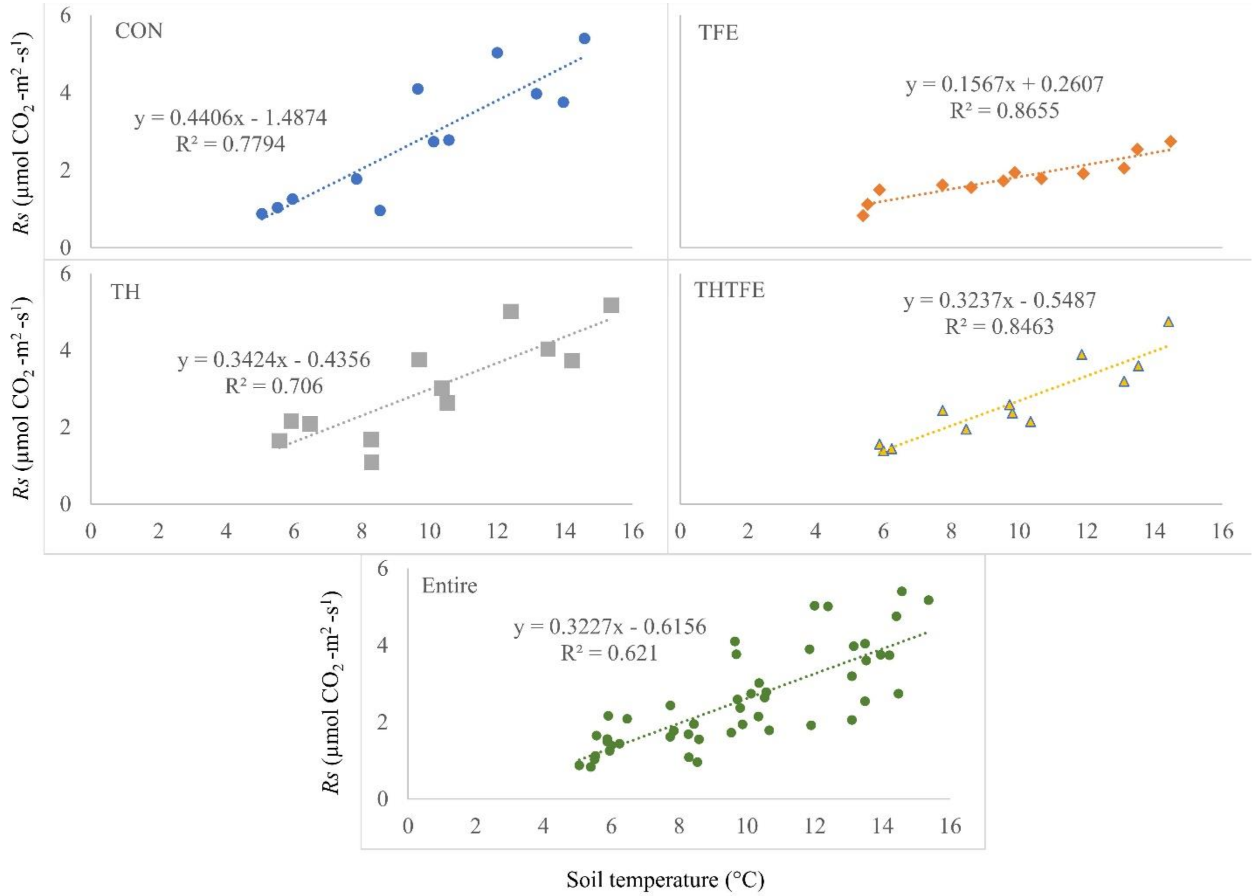

Figure 4. Relationship between soil respiration and soil temperature of each plot and entire plots. CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively. The difference of slopes between treatments were significant, following order CON=THTFE=TH>TFE (*p*<0.05).

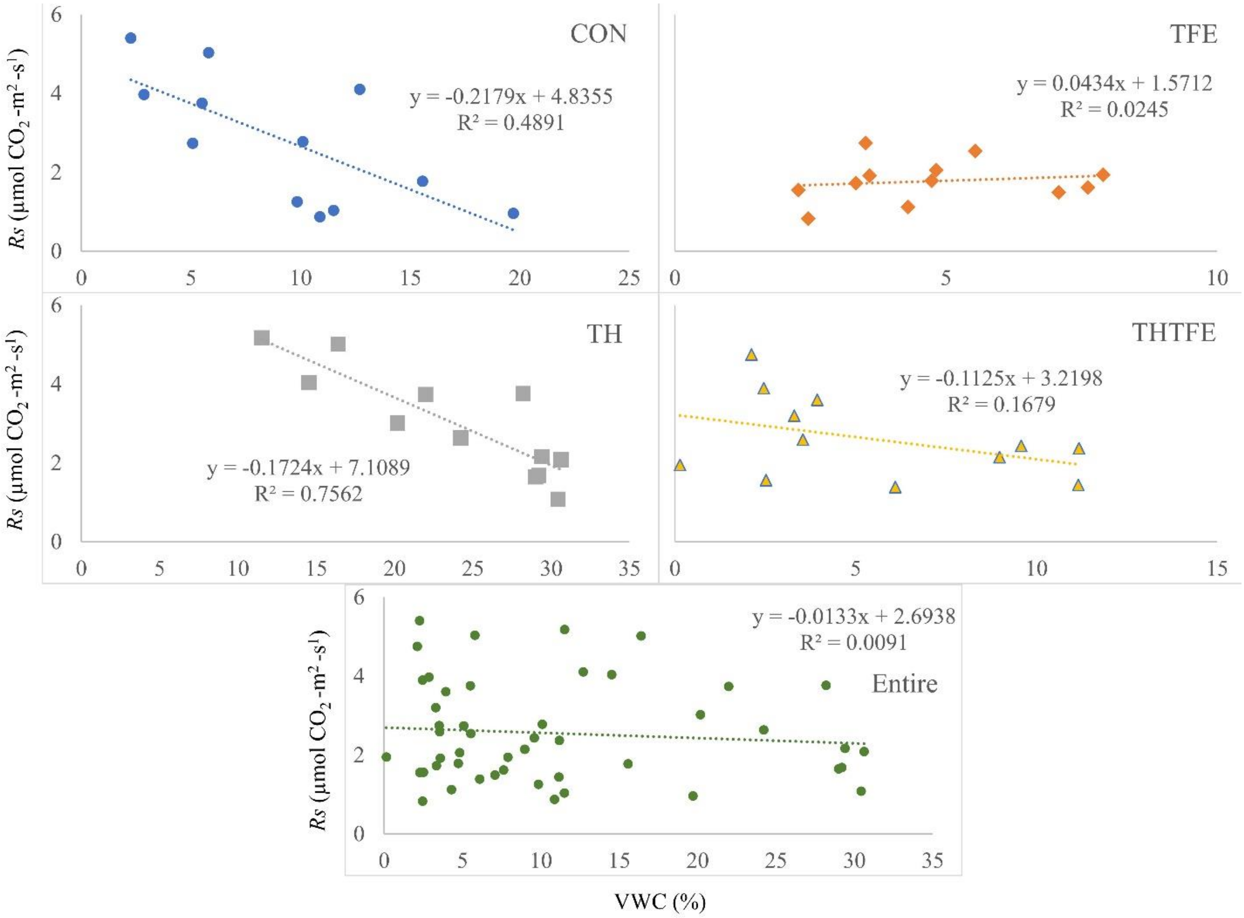

Figure 5. Relationship between soil respiration and volumetric water content of each plot and entire plots. CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively. The difference of slopes between treatments were significant, following order TFE≥THTFE≥TH=CON (*p*<0.05).

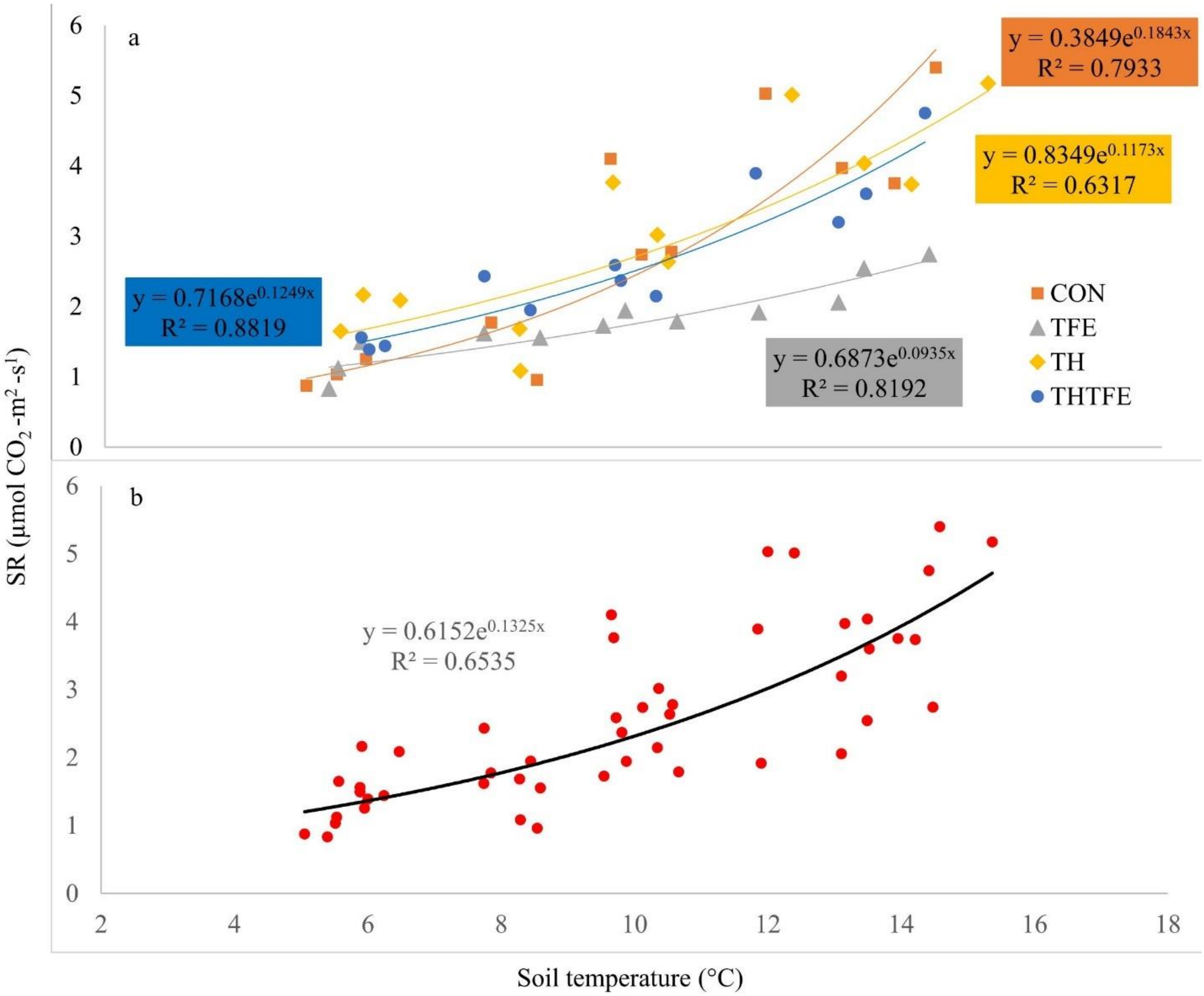

Figure 6. Relation between soil respiration and soil temperature in each plot at -10 cm depth fitted with an exponential model. CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively. a) indicates the Q_{10} model on each treatment, and b) represents the Q_{10} model of entire plots. The difference of slopes between treatments were significant, CON=THTFE=TH>TFE (p<0.05).

Appendix 1

Two supplementary plots were selected to examine the immediate responses (before and after TFE installation)of R_s to two treatments (thinning and TFE) since R_s measurements were not taken prior to panel installation on the Canyon Loop fFrewood site described in Chapter 4. Those two sites are: 1) Canyon loop firewood site, and 2) Clear cut Control site.

Supplementary plot 1.

Canyon loop firewood R_s site

Site description

Additional R_s measurement PVC sampling tubes were installed 20 m away from the CON plot (Figure 1-a) to evaluate the immediate response of R_s to drought treatment without thinning treatment. Ten R_s on each treatment (N=20, n=10) were measured (CON and TFE) from July 2015 to November 2015 with soil temperature (ST) and volumetric soil water contents (VWC). The plot size was 40 x 40 m^2. Tree density on the plot was 419 TPH (67 trees) with 15.1 cm of mean DBH and 26.3 m of height. Each soil PVC sampling tubes between treatment was paired and was separated at least 2 m away. The TFE treatment was set up in August 2015. Two months R_s measurements were taken before TFE panel installation, and then R_s was measured ofr three months were taken after the TFE panel installation. Also, ST and VWC were measured at the same time using methods described in Chapter 4.

Statistical analysis

Monthly mean of R_s, VWC, and ST by treatments were calculated as the mean of ten soil collar measurements. Repeated measures t-test was used to test the differences in R_s, VWC, and ST. All of the tests were performed using R (version, 3.4.4).

Results

Mean of R_s of five months showed no difference between treatments (TFE and CON; Table 1) prior to panel installation. However, R_s was significantly different in September and October after the drought treatment installation compared to the CON ($p < 0.05$; Figure 7). R_s on the two treatments decreased by season changing from summer to fall. TFE decreased R_s by 43 % and 34 % in September and October, respectively, compared with that on CON. Also, TFE lowered VWC significantly. VWC under drought was depressed by around 80 % in September compared with that on CON. However, ST was not different between the two treatments.

Table 1. Five months mean of R_s, VWC, and ST

	R_s	VWC	ST
CON	4.02 ± 0.71^{ns}	8.55 ± 1.84^{a}	10.36 ± 1.62^{ns}
TFE	3.78 ± 1.08^{ns}	4.72 ± 1.85^{b}	10.42 ± 0.92^{ns}

Lowercase letter indicates a significant difference ($p<0.05$)
ns; not significant

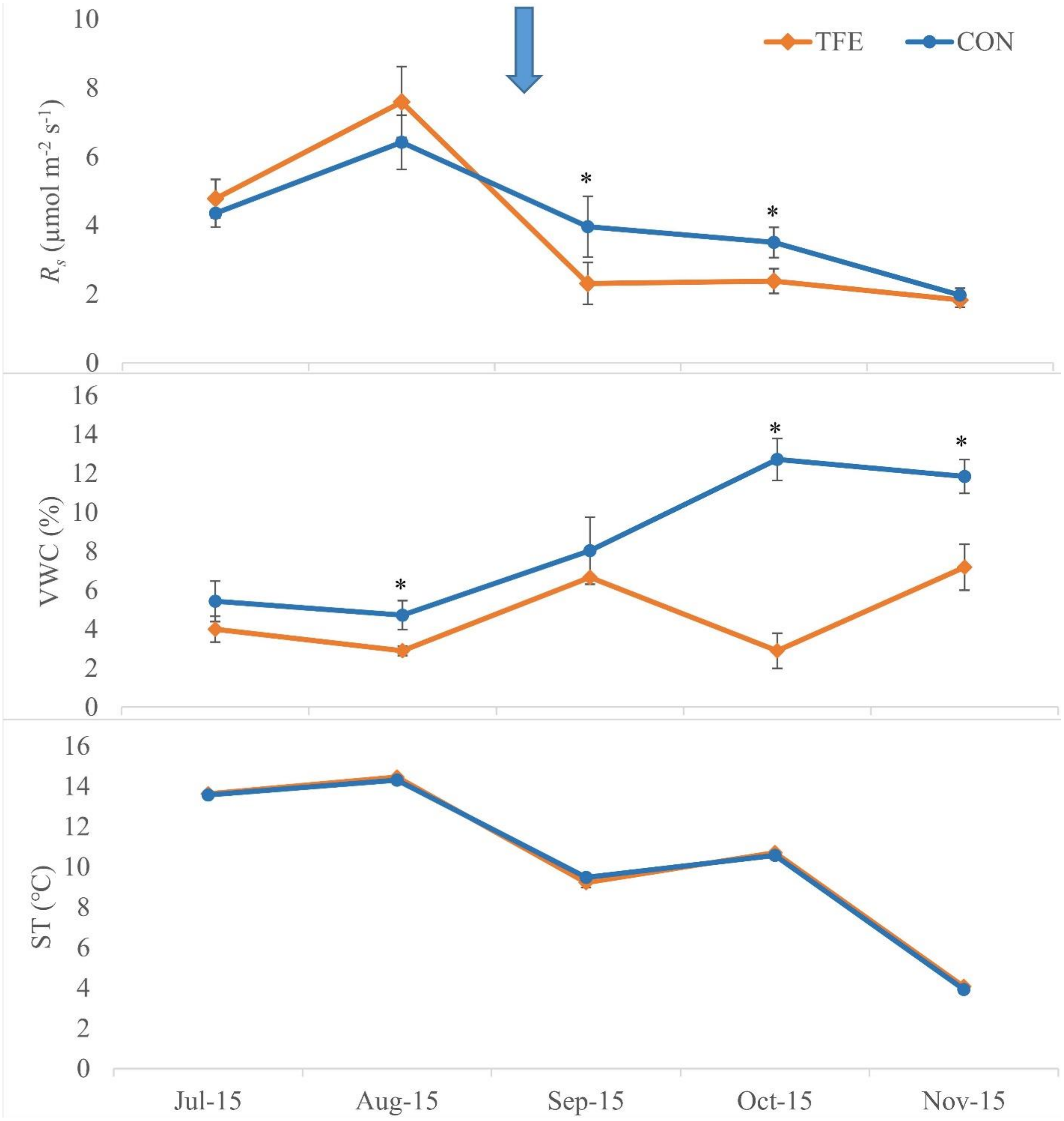

Figure 1. Soil respiration, volumetric water content (VWC) at -10 cm depth, and soil temperature (ST)(c) from July in 2015 to November in 2015 on the additional *Rs* site near TFE study site. A blue arrow means when throughfall exclusion was installed. CON and TFE indicate Control, and Throughfall exclusion, respectively. *indicates significant difference between treatments.

Supplementary plot 2.

R_s on Clear Cut Control stand

Site description

An additional R_s measurement plots was set up on a site called ‘Clear Cut Control’ (lat. 46°50’41.27”N, long 122°16’23.08”W) stand (26-year-old; Figure 1-b) as a replicate to the Canyon Loop Firewood stand. The study was designed as a 2 x 2 factorial with two levels of precipitation. Four 20 x 20 m^2 were set up in September 2015. This site is a replication with two treatments (thinning + TFE) of soil respiration site on canyon loop firewood in Chapter 4. Thinning and drought panel installation on the site were completed in October 2015. Five R_s measurements on each plot were taken from September 2015 to December 2015 (N=20, n=5). Also, ST and VWC were measured at the same time using the same methods in Chapter 4. Tree density and mean DBH of each plot were described in Table 6.

Statistical analysis

Monthly mean of R_s, VWC, and ST by treatments were calculated as the means of Five soil collar measurements. Repeated measures two-way ANOVA was used to test the differences in R_s, VWC, and ST. All of the tests were performed using R (version, 3.4.4).

Results

We found R_s was not different among treatments after treatment installation on Clear Cut Control stand (Figure 8), yet R_s across four treatments decreased after thinning and TFE installation. Although no significantly difference was detected on R_s after treatments, the degree of reduction of R_s on thinned plots was higher than those of unthinned plots. VWC on TH plot was the highest among treatments (Table 7)(Figure 8). VWC on two thinned plots increased after thinning. However, VWC on TFE plot slightly decreased. ST didn’t show any difference among treatments.

Table 1. Stand density and mean DBH on Clear Cut Control site.

Plot	CON	TFE	TH	THTFE
Before thinning				
SD (Trees ha^{-1})	450	475	500	475
DBH (cm)	20.4	19.4	22.1	17.4
After thinning				
SD (Trees ha^{-1})			300	275
DBH (cm)			21.7	21.6

Table 2. Four months mean of R_s, VWC, and ST

	CON	TFE	TH	THTFE
R_s	2.99 ± 0.55 ^{ns}	2.89 ± 0.48 ^{ns}	3.05 ± 0.73 ^{ns}	3.18 ± 0.75 ^{ns}
ST	7.67 ± 1.81 ^{ns}	7.69 ± 1.86 ^{ns}	7.56 ± 1.17 ^{ns}	7.88 ± 1.98 ^{ns}
VWC	20.83 ± 0.73 ^{b}	11.15 ± 0.29 ^{c}	31.96 ± 1.79 ^{a}	16.53 ± 1.63 ^{b}

Lowercase letter indicates a significant difference (p<0.05)
ns; not significant

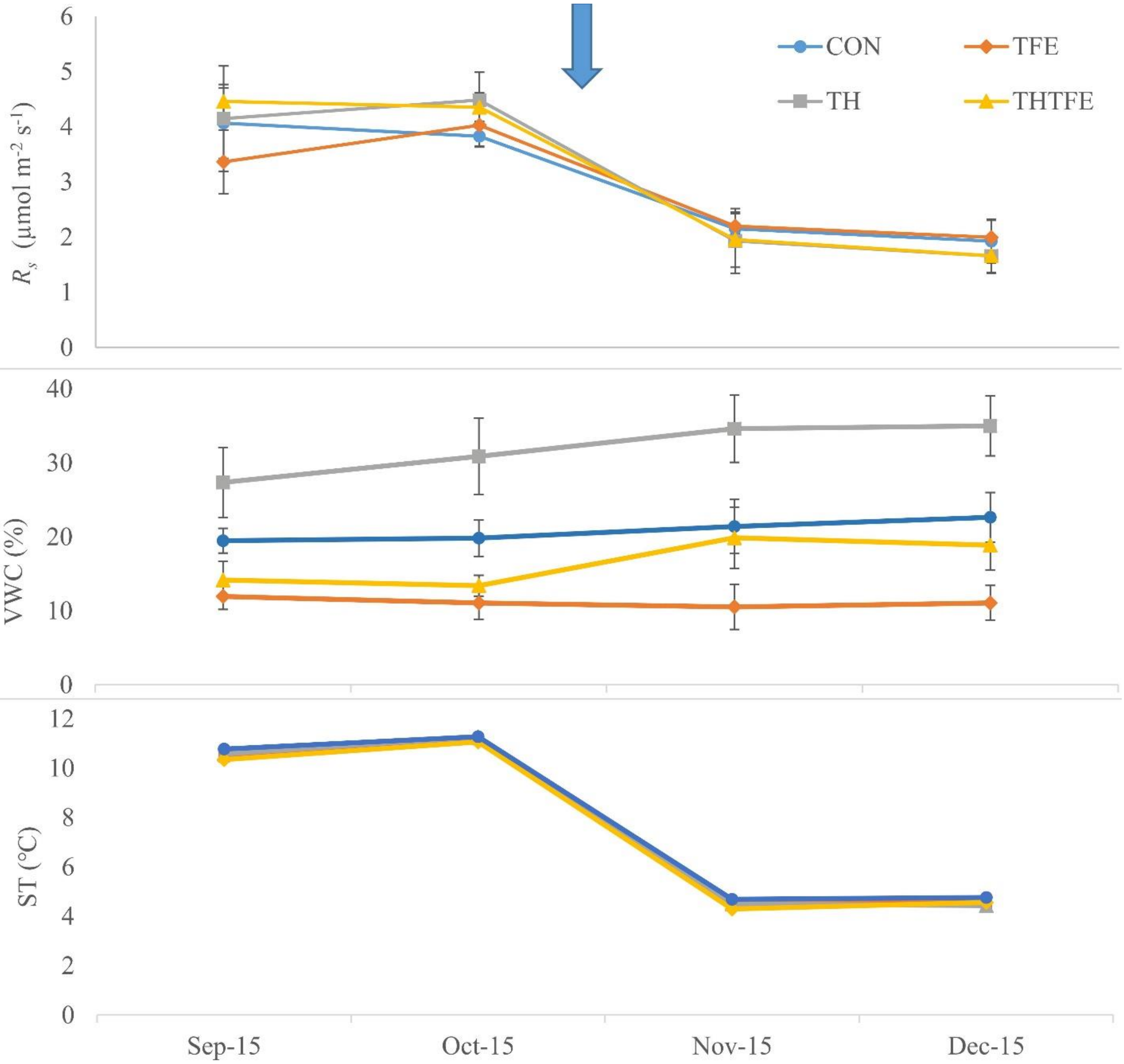

Figure 1. Soil respiration, volumetric water content (VWC) at -10 cm depth, and soil temperature (ST)(c) from September in 2015 to December in 2015 on Clear cut SR site. A blue arrow means when thinning and throughfall exclusion was applied. CON, TFE, TH, THTFE indicate Control, Throughfall exclusion, Thinning, and combination (Thinning and Throughfall exclusion), respectively. *indicates a significant difference between treatments.

Model Comparison

The models between study 1 and study 3 were compared, and we found those models were different. This might be due to site-specific characteristics, thinning intensity, measurement duration, and timing of treatment installation. These two sites have different environmental conditions that thinning applications were carried out on study 3 sites several times owing to study 3 site is wetter than study 1 site. Also, two months of measurements for R_s might not have been enough to determine a decrease in R_s. Moreover, treatments installation (thinning and TFE) completed in November, so differences in R_s after thinning among treatments was likely small during this time of temperature limitation.

CHAPTER 5. Conclusions and Future Directions

Conclusions

The overarching goals of this research were to evaluate the effects of drought stress and silvicultural application (thinning) on tree physiological traits, tree growth, and soil respiration on Douglas-fir plantations, and to assess whether thinning is a possible drought mitigation tool.

Chapters 1 and 2 elucidated Douglas-fir's physiological traits and tree stem growth in response to thinning and drought treatment. We found that thinning enhanced soil volumetric water content and soil water potential and the physiological traits and stem growth of trees. Growth response to thinning was almost immediate, approximately one month earlier than on other treatments, and growth on thinned sites occurred over a longer period of time, with most of the expansion happening earlier in the spring than on unthinned sites. These responses were attributed to less competition of remaining trees for soil water, nutrients, and growing space. In contrast, throughfall exclusion reduced soil volumetric water content and soil water potential and the physiological traits of trees. The drought treatment negatively affected the days of tree stem expansion. The decreases in physiological traits and stem growth were due to the limitation of soil water availability induced by throughfall exclusion. Thinning compensated for the negative effects on stem growth and physiology stress of trees, as we hypothesized. The physiological responses (WUE_i and carbon isotope discrimination) were more sensitive to drought stress than basal area increment. Stem growth and basal area increment showed a different pattern in 2016 as stem growth was reduced by drought more than the control, but basal area increment remained unaffected by drought compared to the control. This difference in growth response is likely due to the different data collection methods; stem growth (stem expansion and contraction) is related to water content, whereas basal area is driven by carbon accumulation related to photosynthesis.

Photosynthesis between the control and throughfall exclusion sites in 2016 were not significantly different, although photosynthesis on the control was higher than that on the throughfall exclusion plot.

Chapter 4 explored the relationship between soil respiration and soil temperature, and soil volumetric water content, and the effects of the two treatments on seasonal soil respiration. We found that soil respiration was positively correlated with soil temperature, but negatively related to soil volumetric water content. Mean Q_{10} on the site was higher than the global average of Q_{10}. Also, the thinning and throughfall exclusion treatments negatively influenced Q_{10}. We found the soil respiration and Q_{10} are sensitive to drought stress. Soil respiration may have been reduced immediately after thinning but reached a level similar to the control after some months, probably due to root growth from carbon accumulation by higher photosynthetic rate under the thinning treatment.

Management Implications

Summer temperature is expected to be + 3.2 °C warmer by 2040 (Mote and Salathe 2010) with more severe and frequent drought expected to decrease growth of Douglas-fir, WA (Littell et al. 2008). If future drought events are mild or not extreme, the growth of Douglas-fir may not decrease, but the physiological traits such as water potential, sapflow, and photosynthesis will decrease. The responses of these physiological traits are more sensitive to drought than tree growth, impaired physiological mechanism by continuous drought could lead to a decrease in tree growth, loss of biomass accumulation, and then tree mortality. The potential for non-growing season photosynthesis to store carbon in the PNW may provide a mechanism for Douglas-fir to adjust to increased seasonal drought; the idea has not been well studied (Lassoie et al. 1985), but may serve as a mechanism to offset summer photosynthesis. We found that thinning increased tree growth and could mitigate the effect of drought on tree growth.

Traditionally, thinning is an intermediate treatment conducted to increase tree growth and production of remaining trees by removing competition for light availability and nutrients under favorable conditions. Thinning can also mitigate drought effects on trees and forests ecosystem under warmer and drier conditions by increasing resistance to drought. Previous studies have found lower tree mortality rates (Ogaya and Peñuelas 2007; Gavinet et al. 2019), increase in tree growth (McDowell et al. 2006) and production (Baleshta et al. 2015) on thinned sites than on unthinned sites and/or sites under drought stress. Chase et al. (2016) suggest that thinning relieves stress, increasing forest health on high density sites with low productivity, while maximizing growth of remaining trees on high density, high productivity sites.

If most plantation sites used for production (high site index) have deep soils and limited drought stress, modest adjustments to stocking may be sufficient to prevent catastrophic losses in productivity with drought. Plantations on lower site indexes with shallow soils, or greater exposure to drought stress may respond differently to increasing drought stress than what we found here, or may require heavier thinning to achieve the same drought reduction.

Future Direction

This study is believed to be the first study utilizing throughfall exclusion in the PNW and provides insights into how thinning and drought influenced Douglas-fir’s growth and physiology in the PNW. Based on this study, follow up research will focus on systematic design, mechanistic understanding of the interactions between environmental changes and plants under drought conditions, and various stand age classes with replications.

This study was conducted on a mature stand so we still do not know how trees in different age classes, nor different initial stocking will respond to the combination of drought and silvicultural applications. Also, the effect of fertilization on drought, another common silviculture treatment in the PNW is unclear. Replications across a strong water availability gradient would increase our understanding of the effects of silvicultural applications and drought on tree growth and physiology. Varying the intensity of thinning would also be useful in determining the range of expected physiological and growth responses to thinning. Nevertheless, this throughfall study provides new information which is useful to predict future responses of trees to drought events, and can provide guidelines for forest management to mitigate against climate changes.

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