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Physiological responses to drought in healthy and stressed trees: a comparison of four species in Oregon, USA

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Oregon, USA

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Master thesis, 30 credits, in *Physical Geography and Ecosystem Analysis*

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ABSTRACT

Four tree species in Oregon (USA) were studied to examine physiological and structural responses to drought stress: ponderosa pine (*Pinus ponderosa*) and western juniper (*Juniperus occidentalis*) in a semi-arid ecoregion, and Douglas-fir (*Pseudotsuga menziesii*) and white oak (*Quercus garryana*) in a mesic coastal ecoregion. This investigation compared the response of paired *healthy* and *stressed* (<10% and \geq 10% canopy loss respectively) trees to drought using leaf and soil water potential as well as tree-ring width data. *Stressed* trees, as indicated by canopy condition, were expected to be more drought stressed but there was generally no significant difference in leaf water potentials between the two categories, although leaf water potentials did vary markedly among species. In some cases *stressed* trees showed more variable growth rates and more sensitive responses to climatic variables than *healthy* trees, suggesting they were predisposed to be more drought stressed than *healthy* trees.

Keywords: Geography, Physical Geography, Water Potential, Tree-rings, Drought

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TABLE OF CONTENTS

1. INTRODUCTION.....	1
2. AIM	3
3. SCIENTIFIC CONTEXT	4
3.1 Oregon climate and drought.....	4
3.2 Tree species	5
3.3 Short-term physiological responses of trees to drought.....	5
3.4 Water potential as a measure of short-term tree drought stress	7
3.5 Long-term physiological response of trees to drought.....	8
3.6 Using tree-rings to measure long-term and retrospective tree drought stress	9
4. RESEARCH HYPOTHESES.....	11
5. METHOD	12
5.1 Climate	12
5.2 Site characteristics and sampling strategy.....	13
5.3 Water potential (Ψ)	17
5.4 Tree-rings	18
6. RESULTS.....	23
6.1 Site climate.....	23
6.1 Water potential (Ψ)	24
6.2 Tree-rings	28
7. DISCUSSION.....	36
7.1 Climatic conditions	36
7.2 Comparing Ψ measurements to expected values	37
7.3 Severe drought stress response at DF.....	38
7.4 The relationship between foliage loss and Ψ	41
7.5 Water potential: methodological issues.....	44
7.6 The response of tree growth to climate	45
7.7 The relationship between foliage loss and tree growth.....	47
7.8 Tree-rings: methodological issues.....	49
7.9 General methodological issues.....	50
7.10 Future research directions	51
8. CONCLUSIONS	52
9. BIBLIOGRAPHY	53

LIST OF ACRONYMS AND SYMBOLS

Symbol or acronym	Definition
BAI	Basal area increment
DF	Douglas-fir site
<i>G</i>	Gini coefficient
JU	Western juniper site
PDO	Pacific Decadal Oscillation
PNW	Pacific Northwest
Ψ	Water potential
Ψ_{leaf}	Leaf water potential
Ψ_{min}	Minimum midday leaf water potential
Ψ_{pd}	Predawn water potential
Ψ_{soil}	Soil water potential
Ψ_{50}	Plant water potential associated with 50% loss of hydraulic conductivity
RWI	Ring-width index
VPD	Vapour pressure deficit
WO	White oak site
YP	Ponderosa pine site

1. INTRODUCTION

Forests cover 31% of the terrestrial land surface and contain ~45% of all terrestrial ecosystem carbon (Bonan 2008; Keenan et al. 2015). Tree growth declines during drought events, and lag effects on growth can occur in subsequent years, which can lead to decreased net carbon uptake (Anderegg et al. 2015; Zhao and Running 2010; Thomas, 2009). For example, European eddy covariance flux tower measurements from forested sites showed an average reduction in gross primary productivity of 30% during the 2003 heatwave, leading many forests to be net sources of CO₂ to the atmosphere and reversing 4 years worth of carbon sequestration (Ciais et al. 2005). Furthermore, severe and/or recurring droughts can lead directly or indirectly (via interactions with fire regimes, pathogens or pests) to tree mortality (Allen et al. 2015; Park Williams et al. 2013). In a meta-analysis of papers published since 1970, Allen et al. (2010) found 88 reported cases of drought-related forest mortality spread over every forested continent. These included reports of increased background tree mortality rates due to rising temperatures and water deficits, as well as an increase in the number of die-off events due to severe drought. It also showed that drought-related tree mortality was occurring across all forest ecosystems, not only those that are generally considered to be water-limited.

Given predictions of higher air temperatures, along with more frequent and longer drought events over the next century (IPCC 2014), it is highly likely that forests worldwide will experience further reductions in growth, increased background mortality rates and more frequent die-off events due to drought in the future (Allen et al. 2015). This could lead to large-scale changes in forest structure and composition as well as to significant changes to the terrestrial carbon sink and feedbacks to climate change (Phillips et al. 2009; Lucht et al. 2006; Jiang et al. 2013). On a global scale, these drought-induced reductions in the carbon sink may be large enough to negate any increase due to carbon and nitrogen fertilization and longer growing seasons (Reichstein et al. 2013).

However, the response of terrestrial ecosystems to climate extremes, including drought, is one of the largest uncertainties in future predictions of the carbon cycle (Sitch et al. 2008). There is debate in the literature over whether forests will be resilient to future drought (due to increased water use efficiency from CO₂ fertilization) or whether they are becoming more vulnerable (due to higher temperatures that exacerbate negative physiological impacts of drought; Allen et al. 2015). Although there is general understanding of the processes leading to tree drought stress and drought-related mortality, the precise physiological mechanisms and thresholds, species traits or climate factors that result in drought stress and drought-related mortality remain elusive (Park Williams et al. 2013; Breshears et al. 2009; Sala et al. 2010; Meinzer et al. 2010; McDowell and Allen 2015). This may be partly due to the difficulty of studying physiological tree drought stress and mortality in situ and in real time (Breshears et al. 2009). Furthermore, tree responses and adaptations to drought vary widely both within and between species and more research is needed to understand these differences (Bréda et al. 2006; Meinzer et al. 2010; van der Molen et al. 2011; Berner and Law 2015). Consequently, it has proven difficult to quantify species drought vulnerability so that it can be incorporated into ecosystem models, which have failed to accurately predict tree drought stress and drought-related mortality (Anderegg et al. 2015; van der Molen et al. 2011; McDowell et al. 2016).

2. AIM

This thesis attempted to address some of these research gaps by collecting data in situ on the response of four tree species to drought as it occurred during summer 2015 in Oregon (USA). Fieldwork was conducted with colleagues from Oregon State University, supporting the work of the Terrestrial Ecosystem Research and Regional Analysis in the Pacific Northwest (TERRA-PNW) group. The aim was to investigate whether trees with greater drought-induced canopy loss also experienced greater physiological drought stress compared to trees with minimal canopy loss, and how these differences varied among species. The four species examined were: Douglas-fir, white oak, western juniper and ponderosa pine.

By selecting trees with canopy loss, it was hoped that the processes leading from drought-stress to drought-related mortality could be captured. The physiological response of trees to drought was measured in the short-term (summer 2015) using leaf and soil water potential and in the long-term (last few decades) using tree-rings. The novel combination of these two datasets enabled an investigation of the current response to drought and how it may have been affected by prior differences in tree growth and climate sensitivity.

3. SCIENTIFIC CONTEXT

3.1 Oregon climate and drought

Oregon has an extremely varied climate due to the presence of the Pacific Ocean (on the western coast) and the Cascade Mountains (running north-south through the state and averaging 1500 m altitude; WRCC 2016). West of the Cascades, the climate is mild and wet (~980-2500 mm mean annual precipitation) due to the proximity of the Pacific Ocean (OCCRI 2010; Law and Waring 1994). East of the Cascades, the mountains' rainshadow produces a semi-arid region (~220-530 mm mean annual precipitation) with a high diurnal temperature range (OCCRI 2010; Law and Waring 1994). In both regions, precipitation falls mainly between October and March and summer droughts are common (OCCRI 2010). Central Oregon (east of the Cascades) is the most drought-prone region in the Pacific Northwest (PNW) region of the US and drought occurrence is often associated with the warm phase of the Pacific Decadal Oscillation (PDO; Knapp et al. 2004; Thomas et al. 2009).

The effects of climate change have already been felt in Oregon and the wider PNW. Average air temperatures in the PNW increased by 0.8°C over the last century (Mote and Salathé 2010) and snowpack has declined approximately 20% since 1950 (Mote et al. 2005). Between 2000-2004, the western US experienced its most extreme drought in at least 800 years (Schwalm et al. 2012). As a result of increasing temperatures and lower soil moisture, increased background forest mortality rates across the western US have been reported (van Mantgem et al. 2009) as well as regional scale die-off events (Breshears et al. 2005). Over the next century, air temperatures in the PNW are predicted to rise on average by 3.0°C (Mote and Salathé 2010). Projections show only minor (1-2%) increases in precipitation over the next century but several models showed stronger seasonality of precipitation with wetter winters and drier summers (Mote and Salathé 2010). Park Williams et al. (2013) predict that forest drought stress in the western US will exceed that of the most severe droughts of the last millennia by 2050.

3.2 Tree species

Four tree species were investigated: Douglas-fir (*Pseudotsuga menziesii*), white oak (*Quercus garryana*), western juniper (*Juniperus occidentalis*) and ponderosa pine (*Pinus ponderosa*). Douglas-fir, ponderosa pine and western juniper are evergreen gymnosperms whereas white oak is a deciduous ring-porous angiosperm. Douglas-fir and ponderosa pine are two of the most common species in western North America and are economically important (Beedlow et al. 2013; Law and Waring 2015). White oak is the most widely distributed oak species in the western US (Franklin and Dyrness 1988). Western juniper has a scattered distribution in the PNW but is most extensive in arid central and eastern Oregon (OSU 2005). The main growing season for all four species is spring and summer (OSU 2005; Beedlow et al. 2013; Oliver and Ryker 2015 ; Gould et al. 2011).

All four species are relatively drought tolerant, with western juniper generally able to survive in the most arid habitats and Douglas-fir in the least arid. White oak and western juniper have deep taproots and extensive rooting systems, respectively. White oak has especially high leaf specific hydraulic conductivity but western juniper and ponderosa pine also maintain low leaf area to sapwood area ratios (Domec et al. 2007; OSU 2005; Maherali and DeLucia 2000). Both ponderosa pine and Douglas-fir maintain relatively tight control of stomatal conductance to limit water loss during drought (Hubbard et al. 2001; Bond and Kavanagh 1999).

3.3 Short-term physiological responses of trees to drought

In the short-term, transpiration and stomatal conductance are key physiological processes that mediate tree response to drought. Transpiration creates a gradient of water potential through the tree, with higher potential at the roots and lower potential at the leaves. Water potential is a measure of the potential energy of water compared to pure water under no pressure at the soil surface (0 MPa; Chapin et al. 2011). During drought, there is a reduction in water potential throughout the plant as evapotranspiration from the leaf stomata and hydraulic resistance of water movement through the soil and roots increases.

At a species-specific threshold leaf water potential, stomata close to avoid further water loss (McDowell et al. 2016). But stomatal closure also limits CO₂ intake, thus decreasing the rate of photosynthesis and carbon accumulation required for tree growth and maintenance. Sustained carbon starvation can lead to tree mortality. For instance, Breshears et al. (2009) showed how widespread pinyon pine mortality occurred in SW US during a severe multi-year drought that caused tree water potential to drop below the point of stomatal closure for at least 10 consecutive months.

However, stomatal closure does not completely stop plant water potential decline, and as it declines the risk of cavitation and embolism increases (Choat et al. 2012). Cavitation occurs when xylem pressures become so low that water vapourizes, causing air bubbles to fill the xylem, potentially to the point of embolism when the xylem is no longer useable for water transport (Tyree and Sperry 1989). The degree to which some species are able to repair embolised xylem elements and the mechanisms involved is debated (Bréda et al. 2006). White oak, Douglas-fir and ponderosa pine have all shown daily cycles of loss and recovery of hydraulic conductivity (Johnson et al. 2009). Tree mortality can occur due to hydraulic failure if a significant proportion of xylem vessels are embolised or damaged (McDowell et al. 2008a). Evidence of drought-related mortality solely due to hydraulic failure comes mainly from experiments with potted plants but also more recently from drought experiments in the Amazon (McDowell et al. 2008a; Rowland et al. 2015).

To avoid drought-induced carbon starvation and hydraulic failure in the short-term, trees not only control stomatal conductivity but also have structural adaptations such as leaf shedding. By reducing leaf area, trees minimize water loss by transpiration, decrease leaf area to sapwood area ratios and increase leaf specific hydraulic conductance at tree level, thus helping maintain sustainable xylem water potentials (Bréda et al. 2006). However, the links between tree physiological processes and leaf shedding and how they affect tree response to drought in different species are still poorly understood (Carnicer et al. 2011).

3.4 Water potential as a measure of short-term tree drought stress

Water potential (Ψ ; MPa) in plants is negative because water is drawn up under tension through the plant against gravity and contains dissolved solutes (Chapin et al. 2011). During the day, water loss from leaves lowers leaf Ψ (Ψ_{leaf} ; Chapin et al. 2011). Midday Ψ_{leaf} is therefore an indicator of maximum leaf water stress (Pérez-Harguindeguy et al. 2013). At dawn, Ψ_{leaf} is expected to have recovered and equilibrated to soil Ψ (Ψ_{soil} ; in the area around the roots) due to shutdown of transpiration overnight (Chapin et al. 2011). Predawn water potential (Ψ_{pd}) can therefore be used as a rough proxy for Ψ_{soil} at the average rooting depth of the tree (Chapin et al. 2011). But research shows that this is not always the case due to night-time transpiration and insufficient plant water recharge overnight (Donovan et al. 1999; Bucci et al. 2004).

Lower values of Ψ_{leaf} and Ψ_{pd} indicate greater plant water stress. Ψ_{leaf} and Ψ_{pd} values are not directly comparable between species because species operate within different ranges of Ψ_{leaf} and Ψ_{pd} . Choat et al. (2012) compiled minimum midday leaf water potential (Ψ_{min}) values for over 200 tree species and found they ranged between -0.5 MPa to -8.6 MPa. Plant Ψ is directly related to hydraulic conductivity: as plant Ψ declines, loss of hydraulic conductivity increases (Tyree and Sperry 1989). The relationship between Ψ and loss of hydraulic conductivity varies among species and is generally non-linear (Tyree and Sperry 1989). In order to compare species, a commonly used index of drought vulnerability is the Ψ at which a plant loses 50% of hydraulic conductivity (Ψ_{50} ; McCulloh et al. 2014). Ψ_{50} values measured in the xylem or leaf for the four species examined are approximately: -1.4 MPa (Douglas-fir), -1.6 MPa (ponderosa pine), -3.6 MPa (white oak) and -9.0 MPa (western juniper; Johnson et al. 2009; Johnson et al. 2012a; Willson et al. 2008).

Species have different hydraulic strategies in terms of how their Ψ is controlled via stomatal closure. These strategies can be described on a continuum from isohydric to anisohydric control of water potential. Isohydric species maintain a constant Ψ_{leaf} by careful stomatal control. Ponderosa pine and Douglas-fir are isohydric species: their midday water potential usually does not drop below -1.45 MPa and -2.5 MPa respectively

(Hubbard et al. 2001; Bond and Kavanagh 1999). Ψ_{leaf} in anisohydric species shows more pronounced fluctuations in response to changes in soil water availability and vapour pressure deficit (VPD; Tardieu and Simonneau 1998). Although the hydraulic strategies of white oak and western juniper have not been characterized, many other oak and juniper species are known to be anisohydric (Meinzer et al. 2013; McDowell et al. 2008b; West et al. 2008). Isohydric species rapidly decrease stomatal conductance to prevent hydraulic failure at the cost of CO_2 uptake, whereas anisohydric species maintain stomatal conductance and CO_2 uptake at the cost of loss of hydraulic conductivity. Therefore theoretically, isohydric species are more vulnerable to drought-induced mortality by carbon starvation, whereas anisohydric species are more vulnerable to drought-induced mortality by cavitation (van der Molen et al. 2011).

3.5 Long-term physiological response of trees to drought

Drought not only reduces tree growth during the drought year but also has repercussions in the following years. Plant tissue damage caused by drought must be repaired or the tissue replaced in order for organs to become fully functional again. Stored carbohydrates, which are already limited due to lower net primary production during the drought year, are thus further depleted during repairs (Bréda et al. 2006). Furthermore, shoot and bud formation (e.g. to replace leaves shed during severe drought) is often a multi-year process and thus trees may not immediately regain full canopy coverage which further contributes to reduced growth (Carnicer et al. 2011).

Other factors also influence the long-term (months to years) response of trees to drought. Trees may adapt to frequent or sustained drought by changing biomass allocation patterns to increase fine root growth, increase sapwood area, decrease leaf area or increase xylem cavitation resistance (McDowell et al. 2008a). Both Douglas-fir and ponderosa pine have shown plasticity in growth rates and traits: trees growing in drier environments show greater drought-tolerance than those growing in wetter area (Maherali and DeLucia 2000; Chen et al. 2010). The climatological characteristics of drought are also important. The impact of drought on trees depends on the length, severity and seasonality of the drought (Anderegg et al. 2013). For example, a mature ponderosa pine stand in Oregon was more

negatively affected by a three-year drought compared to a single year drought due to longer term soil water deficiency and depletion of stored tree carbohydrate reserves (Thomas et al. 2009). The length of time between droughts can also have an important effect, particularly if the interval is shorter than the time needed for trees to fully recover from the effects of a previous drought (Anderegg et al. 2015).

3.6 Using tree-rings to measure long-term and retrospective tree drought stress

Tree-rings allow retrospective analysis of tree growth patterns. Ring-widths are used as estimates of tree growth, where narrow rings indicate poor growth while wider rings indicate a good growth year. Ring-width is affected by many variables including climate, tree age, changes in resource availability, stand management (e.g. thinning) and stand disturbances (e.g. wildfire, insect attack, pathogens; Speer 2010). Rings in temperate and boreal regions are usually produced annually. Cross-dating, the process of assigning calendar year dates to each ring, is a key step in ring-width analysis. Rings are cross-dated by comparing the pattern of narrow and wide rings to other previously dated tree ring chronologies or using known ‘marker years’ that produce a distinctive ring size (e.g. severe drought years that produce very narrow rings; Speer 2010). All four tree species examined in this thesis are known to produce annual rings that are responsive to climate and have been used in prior dendrochronological studies (Gildehaus et al. 2015; Knapp et al. 2004; Park Williams et al. 2013).

Due to the long time series and annual resolution of tree-rings they have often been used to study the impact of drought on tree growth. For example, Anderegg et al. 2015 used a database of tree-ring widths from 1338 sites in the Northern Hemisphere and found a ~9% decrease in tree growth in the first year following a drought with significant decreases in growth lasting up to 4 years after a severe drought event. Ogle et al. 2000 and Suarez et al. 2004 examined drought-related tree mortality and were able to predict the likelihood of death based on patterns of growth variation and mean growth rate in tree rings. In Oregon, western juniper tree-ring measurements have also been used to characterize the historical occurrence of drought (Knapp et al. 2004) and both western

juniper and ponderosa pine tree-rings were used to investigate how drought impacts varied among forest types along a steep gradient in water availability (Berner and Law 2015).

4. RESEARCH HYPOTHESES

To explore the relationship between foliage loss and drought stress, this thesis investigated the following hypotheses:

1. *Summer 2015 weather conditions were hotter and drier compared to 1981-2010 normals which led to significant reductions in tree leaf and soil water potential.*

Across Oregon, snowpack was 40-90% below average during the winter 2014-2015 (USDA 2015) and it was one of the warmest winters on record (OSU 2015). These conditions suggested that severe drought would continue during the summer months (USDA 2015). As a result it was expected that all species would show substantial reductions in Ψ_{pd} and midday Ψ_{leaf} over the course of the summer and compared to literature values from pre-drought conditions.

2. *Trees with greater foliage loss suffered greater drought stress compared to trees with little foliage loss during the summer 2015.*

Comparing pairs of *healthy* and *stressed* trees (according to proportion of canopy loss), it was expected that *stressed* trees would have lower Ψ_{pd} and midday Ψ_{leaf} than *healthy* neighbours since canopy loss is a sign of drought stress (Bréda et al. 2006). *Stressed* trees would therefore also be operating closer to or at negative values in relation to Ψ_{50} compared to *healthy* neighbours.

3. *Trees with greater foliage loss experienced lower rates of growth, more variable growth and responded more sensitively to climate prior to 2015 compared to trees with little foliage loss.*

It is expected that *stressed* trees would show lower mean ring-width and higher growth variability than *healthy* neighbours. *Stressed* trees were also expected to show greater reductions in ring-width during previous drought years as well as higher and more significant correlations to climate variables since they may have been more sensitive to climate than *healthy* neighbours. Reductions in mean growth, higher growth variability and sensitivity to climate have all been linked to drought stress and drought-related tree mortality (Ogle et al. 2000; Suarez et al. 2004).

5. METHOD

The data collection for this thesis was carried out in cooperation with colleagues from the TERRA-PNW group at Oregon State University in Corvallis, Oregon. Fieldwork took place from mid-June to early September 2015.

5.1 Climate

Climate data were from the PRISM Climate Group (Parameter-elevation Relationships on Independent Slopes Model; <http://www.prism.oregonstate.edu/>) which interpolates climate data from over 10 000 surface stations to 4km and 800m gridcells across the conterminous United States (Daly et al. 2008). The 4km resolution was used because more data were available at this resolution.

The Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2010) was used to quantify the severity of drought in climate and tree-ring analyses. SPEI is calculated as precipitation (P) minus reference evapotranspiration (RET). RET is the rate of evapotranspiration from a reference surface and is calculated based on the climate at the specified location. SPEI thus compares water availability (P) with atmospheric water demand (RET). SPEI was selected because it is available in near real time from Western Wide Drought Tracker (<http://www.wrcc.dri.edu/wwdt/time>), using input data from PRISM and the Thornthwaite method (Thornthwaite 1948) to calculate RET. Furthermore, it is multi-scalar (temporally) and ‘standardized’ so values of SPEI are equivalent even when it is calculated over different time scales or in different locations. This was an important consideration in choosing SPEI as a drought index since it was used to compare droughts in four study sites and over time scales ranging from months to years.

T-tests were performed to test for significant differences between 2015 weather and average climatic conditions (based on PRISM climate normals from 1981-2010) using total precipitation and mean air temperature. Differences were tested using summer (June-September) data, the period when physiological measurements were taken in the

field, and growing year (October-September) data, representing the hydrological and botanical growing year for the tree species being investigated (following the example Berner and Law 2015).

5.2 Site characteristics and sampling strategy

Data were collected at four sites in Oregon, each representing a different species (Table 1): DF (Douglas-fir), WO (white oak), YP (ponderosa pine) and JU (western juniper). Two sites (DF and WO) were located on the western side of the Cascades with a mesic climate and two sites (YP and JU) were located on the eastern side of the Cascades with an arid climate (Figure 1). YP was an open stand of young ponderosa pine (~17 years old). JU was an open stand of western juniper (~100 years old) with a few mature ponderosa pine. DF was a dense plantation of young Douglas-fir trees (~30 years old) with a few scattered Douglas-firs in an adjacent open grassy area. The site was located near a residential neighborhood in Corvallis, Oregon. WO was a large park on the outskirts of Corvallis with mixed grassland and forested areas which included white oak and Douglas-fir stands.

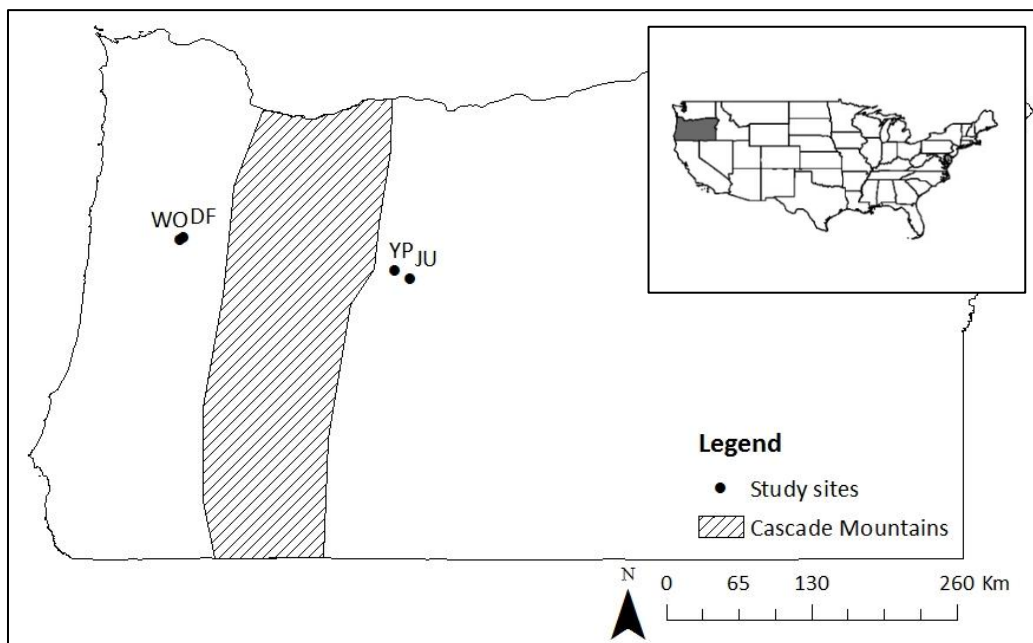


Figure 1. Map of Oregon showing the location of the four study sites (WO=white oak, DF= Douglas-fir, YP=ponderosa pine and JU=western juniper). Inset map shows the coterminous USA with Oregon highlighted in dark grey. Based on data from: <https://www.census.gov/geo/maps-data/data/tiger-cart-boundary.html>

Table 1. Study site location, average annual climate characteristics (based on 1981-2010 normals, ± 1 SD) and dominant species.

Site characteristic	DF	WO	JU	YP
Latitude	44.60	44.57	44.26	44.32
Longitude	-123.31	-123.34	-121.48	-121.61
Altitude (m)	103	163	994	996
Mean annual air temperature ($^{\circ}$ C)	11.4	11.1	8.1	7.7
	± 0.5	± 0.5	± 0.6	± 0.6
Mean annual precipitation (cm)	115.2	128.9	36.2	50.3
	± 27.4	± 29.7	± 9.36	± 12.7
Dominant tree species (common name)	<i>Pseudotsuga menziesii</i> (Douglas-fir)	<i>Quercus garryana</i> (white oak)	<i>Juniperus occidentalis</i> (western juniper)	<i>Pinus ponderosa</i> (ponderosa pine)

The YP site was part of the AmeriFlux network of core sites maintained by the TERRA-PNW group. The JU site was also recently established by the group and both sites follow the same sampling methodology. Descriptive site data including tree height and diameter at breast height (DBH), leaf area index (LAI), specific leaf area (SLA), stem wood density, sapwood area and leaf carbon and nitrogen content were collected from a network of four circular plots following pre-established protocols (Berner and Law 2016; Table 2). The DF and WO sites were later additions to the thesis project and were not part of the TERRA-PNW permanent sampling network, so descriptive site data were not gathered using the same sampling strategy as the other two sites. Instead, at the DF and WO sites, the data were only collected from 10 trees used for Ψ measurements (Table 2). LAI data were collected from two 50m transects that traversed the forest stand and open areas of the sites.

Ψ and sapflow data were collected from paired *healthy* and *stressed* trees at each site which were located close together and had similar DBH and height. Trees were classified as *healthy* if they exhibited <10% canopy loss, or as *stressed* if they exhibited $\geq 10\%$ canopy loss at the top of the canopy (Figure 2). This threshold value was based on field observations: 10% was the value at which the proportion of canopy loss was clearly visible and noticeable to field crew members. Paired *healthy* and *stressed* trees did not differ significantly ($\alpha=0.05$) in height or DBH according to a Wilcoxon signed rank test ($P > 0.05$ at all sites). The proportion of canopy loss of each tree was assessed once at the

beginning of the field season (late June/early July) visually by 2-3 fieldcrew members and compiled into an average. Following the methodology of Koepke et al. (2010), canopy loss was estimated based on the amount of prematurely brown foliage and foliage-less branches at the top of a tree, since this was likely to be canopy lost due to drought (rather than from ageing or shading).

At JU, Ψ and sapflow data were collected on 3 *stressed* and 3 *healthy* trees. At YP, the data were collected from 2 *stressed* and 10 *healthy* trees (later put into pairs used in this analysis). Only a small sample size was used due to the time intensiveness of the Ψ measurements and because all the trees had to be located within a few meters of the same data logger. Unfortunately, due to an error in the installation of the sapflow instruments, these data were unusable and were not included in this thesis. At WO and DF, Ψ measurements were performed on 5 *healthy* and 5 *stressed* trees. No sapflow data was available for these sites due to lack of equipment and risk of theft or damage to the equipment since the sites were located on public land.

Ideally, the tree cores (used for tree-ring analysis) would also have been collected from the same trees as the sapflow and Ψ data. However, taking tree cores would have disturbed the sapflow measurements. At YP, no other *stressed* trees were found at the site apart from the sapflow trees, therefore no tree-ring data were collected. At JU, 5 other *stressed* trees from around the site were cored and these were matched to 5 *healthy* trees from within the plots which had statistically similar height and DBH (paired t-tests, $P > 0.05$ in both cases). At DF and WO, since no sapflow measurements were being taken, the tree cores were extracted from the same 10 trees as used for Ψ measurements.

Healthy and *stressed* trees used for Ψ measurements showed large differences in foliage loss at all sites (Figure 3; though they were only statistically significant at WO based on Wilcoxon signed rank test). Average *healthy* canopy loss was 3% while average *stressed* canopy loss was 41% but reached up to 95% at the JU site. The *stressed* trees at the dry sites had higher average canopy loss than the mesic sites.



Figure 2. Examples of pairs of healthy and stressed trees. Left is the DF (Douglas-fir) site, with the healthy tree on the left, and stressed tree on the right. Right is the JU (western juniper) site, with healthy tree in the background (right) and stressed tree in the foreground (left). Photos taken in August 2015.

Table 2. Characteristics of the trees at each of the study sites. All numbers are averages \pm 1 SD. Averages were compiled based on the 10 trees measured at DF and WO, and 10 randomly selected trees at JU and YP. DF=Douglas-fir, WO=white oak, JU=western juniper, YP=ponderosa pine.

Characteristic	DF	WO	JU	YP
Age (yrs)	32.20 \pm 5.51	59.80 \pm 19.69	108.30 \pm 23.41	16.67 \pm 2.27
DBH (cm)	26.06 \pm 4.73	31.40 \pm 5.04	24.15 \pm 7.45	21.11 \pm 4.76
Height (m)	15.47 \pm 3.32	12.74 \pm 5.19	8.91 \pm 1.87	7.94 \pm 1.44
Wood density (g/cm ³)	0.41 \pm 0.04	0.71 \pm 0.03	0.45 \pm 0.04	0.43 \pm 0.09
Leaf C (%)	49.59 \pm 0.35	45.49 \pm 0.60	48.88 \pm 0.58	48.91 \pm 0.47
Leaf N (%)	1.33 \pm 0.18	2.09 \pm 0.12	0.76 \pm 0.07	1.21 \pm 0.15
SLA (cm ² /g)	70.73 \pm 7.11	74.23 \pm 9.39	28.50 \pm 2.51	42.00 \pm 6.04

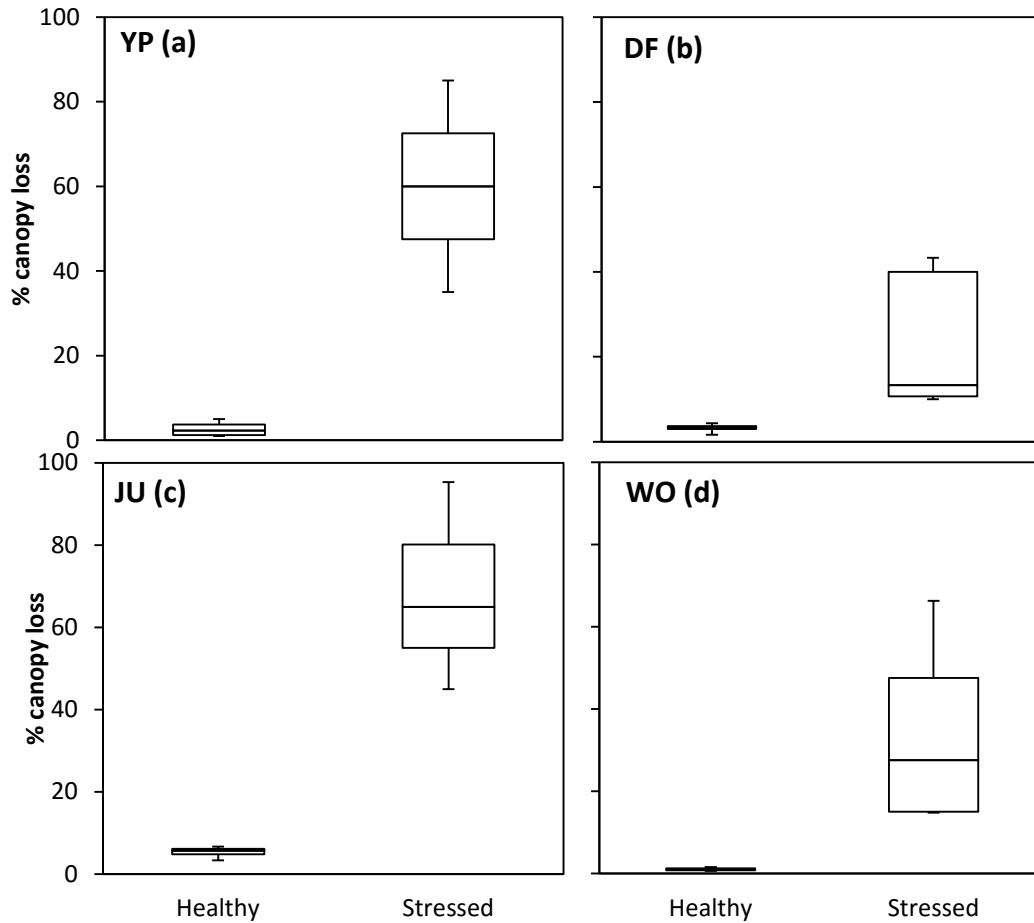


Figure 3. Box plot showing proportion of canopy loss for *healthy* and *stressed* trees used for Ψ measurements at each site. YP=ponderosa pine, DF=Douglas-fir, WO=white oak, JU=western juniper

5.3 Water potential (Ψ)

Ψ_{pd} and midday Ψ_{leaf} were measured monthly at each of the sites (June-August at YP and JU; July-September at DF and WO). Ψ was only measured when no precipitation had fallen at least 24 hours prior to measurements starting. Ψ was measured on 3, 2, 5 and 5 pairs of *healthy* and *stressed* trees at JU, YP, DF and WO, respectively. Ψ_{pd} measurements were completed before sunrise (0300-0600) and midday Ψ_{leaf} measurements were completed during the hottest part of the day (1400-1600) to capture maximum plant water stress. Two needle fascicles or small twigs were measured from each tree following standard procedures outlined by Pérez-Harguindeguy et al. (2013). Samples were extracted from the south-facing (or sun-exposed) side of the tree at mid-

canopy height to provide an average estimate of Ψ from leaves in ‘optimal’ growing conditions (Pérez-Harguindeguy et al. 2013). The height at which samples were excised from the tree was recorded using a laser rangefinder for gravity potential correction. Since Ψ_{pd} represents Ψ_{soil} , Ψ_{pd} measurements were corrected for the effect of gravity by deducting 0.01 MPa per metre height of the sample (Richter 1997).

Ψ was measured using a pressure chamber (PMS Instruments, 1970) with readings down to -4 MPa. A new pressure chamber (Model 1505D, PMS Instruments) was purchased in September which could measure down to -10 MPa. The new pressure chamber was only used for Ψ measurements in September at the WO and DF sites. The two pressure chambers were tested to ensure they gave the same Ψ measurements when the same plant sample was measured in both chambers. No significant difference was found in measurements of the midday Ψ_{leaf} of 5 Douglas-fir twigs whether using the old or new pressure chamber ($W=7$, $p=0.584$).

Wilcoxon signed rank tests were performed on Ψ data at each site to test for significant differences in midday Ψ_{leaf} , Ψ_{min} , and Ψ_{pd} between *healthy* and *stressed* trees. The same test was used to assess the significance of declines in Ψ_{pd} and midday Ψ_{leaf} over the summer between July and August (when measurements occurred at all four sites). Finally Spearman’s rank correlation was used to investigate the relationship between proportion of canopy loss and Ψ_{min} and Ψ_{pd} .

5.4 Tree-rings

Tree cores were collected from 5 pairs of *healthy* and *stressed* trees at DF, WO and JU. At YP, no *stressed* trees were available for tree coring. Two cores were taken from each tree, at 90° angles to each other, providing a total of 60 cores from 30 trees. The tree cores were prepared according to standard techniques outlined by Speer (2010).

The tree-rings from the three sites were visually cross-dated, using known drought years as marker years and reference chronologies (only available for JU; Speer 2010). The width of annual tree-rings was measured using a stereoscopic microscope, Velmex

sliding stage and MeasureJ2X software. Statistical cross-dating for each chronology was performed in COFECHA (Grissino-Mayer 2001) and R (R Development Core Team 2015) using the Dendrochronology Program Library in R (dplR) package (Bunn 2008). Tree cores were compiled into separate chronologies (using mean ring-width for every calendar year) for the group of *healthy* and *stressed* trees from each site. For use in the climate analysis, each chronology was detrended (to remove age-related growth trends and standardize measurements as a ring-width index, RWI; Speer 2010) using splines with a 20 year window (the length of the shortest series) and 0.5 response frequency. One series from JU was detrended with a spline with a 54 year window because the shorter windows failed to remove the growth trend and produced negative RWI values.

Descriptive statistics were calculated for each of the chronologies. These included the Expressed Population Signal (EPS, Equation 1), a measure of the common growth signal expressed by all the tree cores in the chronology (Cook and Briffa 1992).

$$EPS = \frac{N\bar{r}}{\bar{r}(N-1) + 1} \quad (1)$$

Where N is the average number of trees (for each year) and \bar{r} is the effective chronology signal which takes into account the within- and between-tree correlations according to Equation 2 (Cook and Briffa 1992).

$$\bar{r} = \frac{\bar{r}_{bt}}{\bar{r}_{wt} + \frac{1 - \bar{r}_{wt}}{c}} \quad (2)$$

Where \bar{r}_{bt} is the mean interseries correlation between all series from all different trees (Equation 3), \bar{r}_{wt} is the mean correlation between series from the same tree averaged over all trees and c is the total number of cores. The mean interseries correlation (\bar{r}_{bt}) between all tree cores from all different trees (Equation 3; Cook and Briffa 1992) was also estimated as a measure of the similarity of the pattern of growth between all trees.

$$\bar{r}_{bt} = \frac{1}{N_{bt}} (\bar{r}_{tot} \bar{N}_{tot} - \bar{r}_{wt} N_{wt}) \quad (3)$$

Where N_{bt} is the total number of correlations minus the number of within tree correlations (when a tree has more than one core), \bar{r}_{tot} is the average correlation between all tree cores, \bar{N}_{tot} is the average number of within tree and between tree correlations and N_{wt} is the number of within tree correlations.

To assess differences in the variability of ring-widths between *healthy* and *stressed* trees, the Gini coefficient (G , Equation 4) was calculated for individual *healthy* and *stressed* trees at each site (Biondi and Qeadan 2008). G is the sum of the absolute differences between all pairs of observations (in this case, ring-width) scaled by mean and sample size.

$$G = \frac{\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|}{2n^2 \bar{x}} \quad (4)$$

Where x_i and x_j are pairs of observations, n is the sample size and \bar{x} is the mean of the observations. G was calculated for the longest time period common to all trees at each site: 1994-2014 (DF), 1976-2014 (WO), 1933-1952 (JU). The time period of analysis at JU ends in 1952 because no annual rings were visible on some *stressed* trees after this point. Wilcoxon signed rank tests using pairs of *healthy* and *stressed* trees from each site tested for significant differences in G between the two categories.

To assess differences in annual growth rate between *healthy* and *stressed* trees, raw tree-ring widths were converted to basal area increments (BAI; total area of wood growth per year). BAI was calculated using the DBH (minus double the bark width) for each tree, assuming a perfectly circular cross-section, using a preset function in dplR. Bark width was measured for all trees with calipers during tree coring, except for JU *stressed* trees in which case bark width was modelled based on a linear regression of bark width versus

DBH using data from the JU *healthy* trees ($r^2 = 0.72$). Average BAI was calculated for the longest time period common to all trees at each site: 1994-2014 (DF), 1976-2014 (WO), 1933-1952 (JU). Paired t-tests tested for significant differences in BAI between *healthy* and *stressed* trees at each site. Using the DF and WO tree series, paired t-tests were also performed to test for significant differences in tree growth for each year between 1995-2014 to understand whether short-term differences in tree growth may have affected the response of trees to drought in 2015. This test could not be conducted for trees from the JU site since the *stressed* trees stopped producing visible growth rings prior to 2015.

The chronologies were correlated against climate data for each site to investigate how tree growth responded to climate and whether there were significant differences in correlations between *healthy* and *stressed* trees. Before performing the correlations, first order temporal autocorrelation was removed from the chronologies and climate data using ordinary least squares autoregressive (AR) models if necessary and residuals were verified to ensure no first order autocorrelation remained. The series were checked for stationarity (an assumption of AR models) using an Augmented Dickey-Fuller test. In some cases, the series showed spikes of significant autocorrelation at orders >1 . Attempts were made to remove this higher order autocorrelation but it was difficult to estimate the correct order of the ARIMA model needed and the residuals were often still autocorrelated, therefore only significant first order autocorrelation was removed. Before performing the correlations, the chronologies and climate data were normalized.

The chronologies were correlated against climate variables (total precipitation and minimum, mean and maximum air temperature) using Spearman's rank correlation. Correlations were performed at three timescales: annually, seasonally and monthly. Annual correlations used climate variables averaged over the growing year (October – September), following the example of Berner and Law (2015). Seasonal correlations used the following seasons: October-December (autumn), January-March (winter), April-June (spring) and July-September (summer). Correlations were performed for both climate in the current year of ring growth and the prior year. Correlations at each site were

performed on 20 year periods to ensure consistency: 1995-2014 (DF and WO) and 1933-1952 (JU).

To further investigate how trees responded to drought occurring over different time scales and during different parts of the growing year, the chronologies were correlated against SPEI aggregated over 72 months, 36 months, 12 months, 6 months winter (October-March) and 6 months summer (April-September). The same time windows were used as for the correlations against the other climate variables.

Superposed epoch analysis (SEA) was also performed to understand whether significant differences in tree growth occurred during, and in the 3 years after, significant drought events. SEA calculates the deviation from the mean value of a time series for a certain number of years prior to, during, and after 'event' years (Lough and Fritts 1986). To determine whether the mean ring-width during these years was significantly different from mean ring-width in other years, bootstrapped resampling (10000 samples) was used. In this case, the 'event' years were the 3 worst drought years occurring during the longest time period common to all trees at each site (DF= 1994-2014; WO=1976-2014; JU=1933-1952). The drought years were selected using the 12 month SPEI at each site (since this SPEI time series showed the most significant correlation to tree growth; Table 8). 'Event' years were defined as the 3 worst drought years because other selection criteria (e.g. 1 or 2 standard deviations below the mean) resulted in too many or too few 'event' years being selected. Furthermore, the 3 worst years were of similar magnitude at each of the sites (mean SPEI of drought event years: JU=-1.6, DF=-2.1, WO=-2.2). The event years were 1994, 2001 and 2005 (DF); 1977, 2001 and 2005 (WO); and 1934, 1939 and 1949 (JU).

6. RESULTS

6.1 Site climate

As part of the investigation of hypothesis 1, the 2015 weather conditions were compared to 30 year climate normals at each of the sites to show that drought was occurring during and prior to summer 2015, and that this would lead to reductions in Ψ . The 2015 summer (June-September) weather conditions at the four study sites was up to 1.5 °C warmer and the sites received 28-46% less precipitation than the 30 year (1981-2010) average (Table 3). T-tests confirmed that at all four sites, the 2015 summer mean air temperature and total precipitation was significantly higher and lower, respectively, than baseline values ($p < 0.001$ in all cases). Figure 4 shows that June-September were the hottest months of the 2015 growing year at all sites and that June temperatures were well above their normal range. Winter (December-March) air temperatures were also high or above the normal range. At all the sites there were some spring and summer months during 2015 when precipitation was considerably lower than average (Figure 4). Comparisons of growing year (October-September) weather data also showed significantly higher mean air temperatures and lower total precipitation values at all the sites ($p < 0.01$ in all cases).

The 2015 summer SPEI was between -2.33 and -1.21 while the growing year SPEI was between -1.95 and -1.22 at the four sites, indicating significant drought conditions. The arid sites (JU and YP) had lower SPEI than the mesic sites (DF and WO). The summer 2015 drought was the second worst in the last 100 years at the YP and JU site, with only 2003 having slightly lower SPEI (-2.36). At DF and WO, the summer 2015 was the eighth worst drought in the last 100 years. The drought began in 2014 or late 2013 since SPEI was < -1 at all sites during the 2014 summer and growing season but fluctuated around 0 during 2013.

Table 3. Summer (June-September) mean monthly air temperature and summer total precipitation in 2015 and for climate normal based on 1981-2010 monthly data. Standard deviation of the climate normal data is in brackets. DF= Douglas-fir, WO=white oak, JU=western juniper, YP=ponderosa pine.

Site	Mean summer air temperature 2015 (°C)	Mean summer air temperature 1981-2010 (°C)	Total summer precipitation 2015 (mm)	Mean summer total precipitation 1981-2010 (mm)
DF	19.0	17.6 (0.5)	63.7	93.3 (40.3)
WO	18.6	17.3 (0.6)	69.6	93.5 (42.1)
JU	17.2	15.7 (0.8)	27.4	50.3 (24.6)
YP	16.5	15.1 (0.7)	30.6	56.2 (25.3)

6.1 Water potential (Ψ)

At the dry sites (JU and YP), Ψ_{pd} and midday Ψ_{leaf} declined between June and August, with minimum values occurring in August (Figure 5). The pattern matches the weather data from the two sites (Figure 4) which show that the hottest temperatures and lowest precipitation occurred in August. During the summer, mean air temperature and total precipitation changed little at the two sites, suggesting that Ψ declined due to the sustained hot and dry conditions.

At the mesic sites (DF and WO), Ψ_{pd} and midday Ψ_{leaf} declined between July and September (Figure 5), also due to sustained high air temperatures and low precipitation (Figure 4). At WO, Ψ remained low in September whereas at DF, Ψ of the *healthy* trees recovered. Differences in the September Ψ at the two sites were due to the DF measurements being made two weeks later than the WO measurements, during which time 25 mm of precipitation fell at the site, the most significant amount of precipitation for any two week period during the summer (June-September).

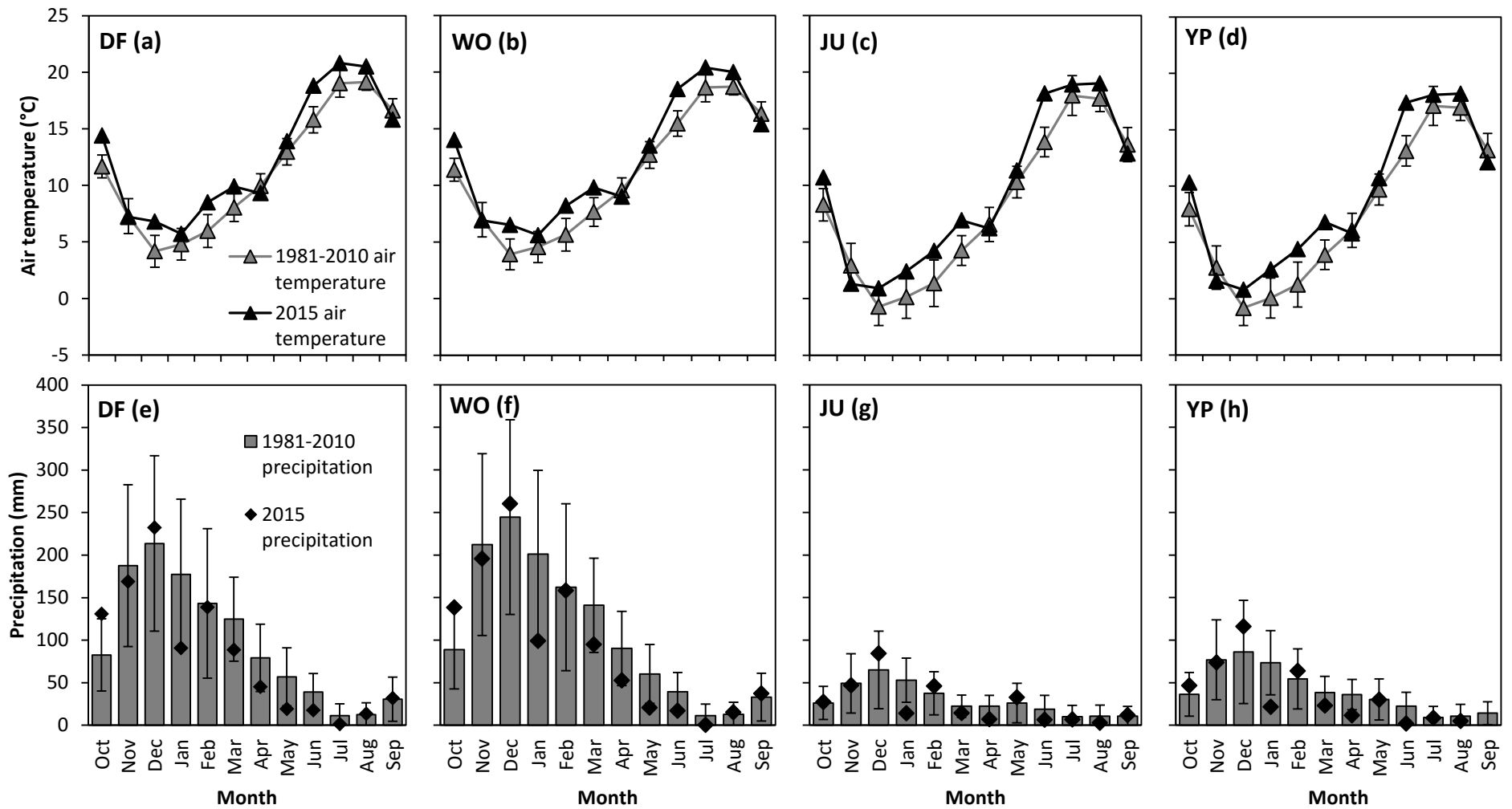


Figure 4. Mean monthly air temperature (a-d) and precipitation (e-h) for the four study sites during the growing year 1981-2010 normals and 2015. Error bars are standard deviation. DF=Douglas-fir, WO= white oak, JU=western juniper and YP=ponderosa pine.

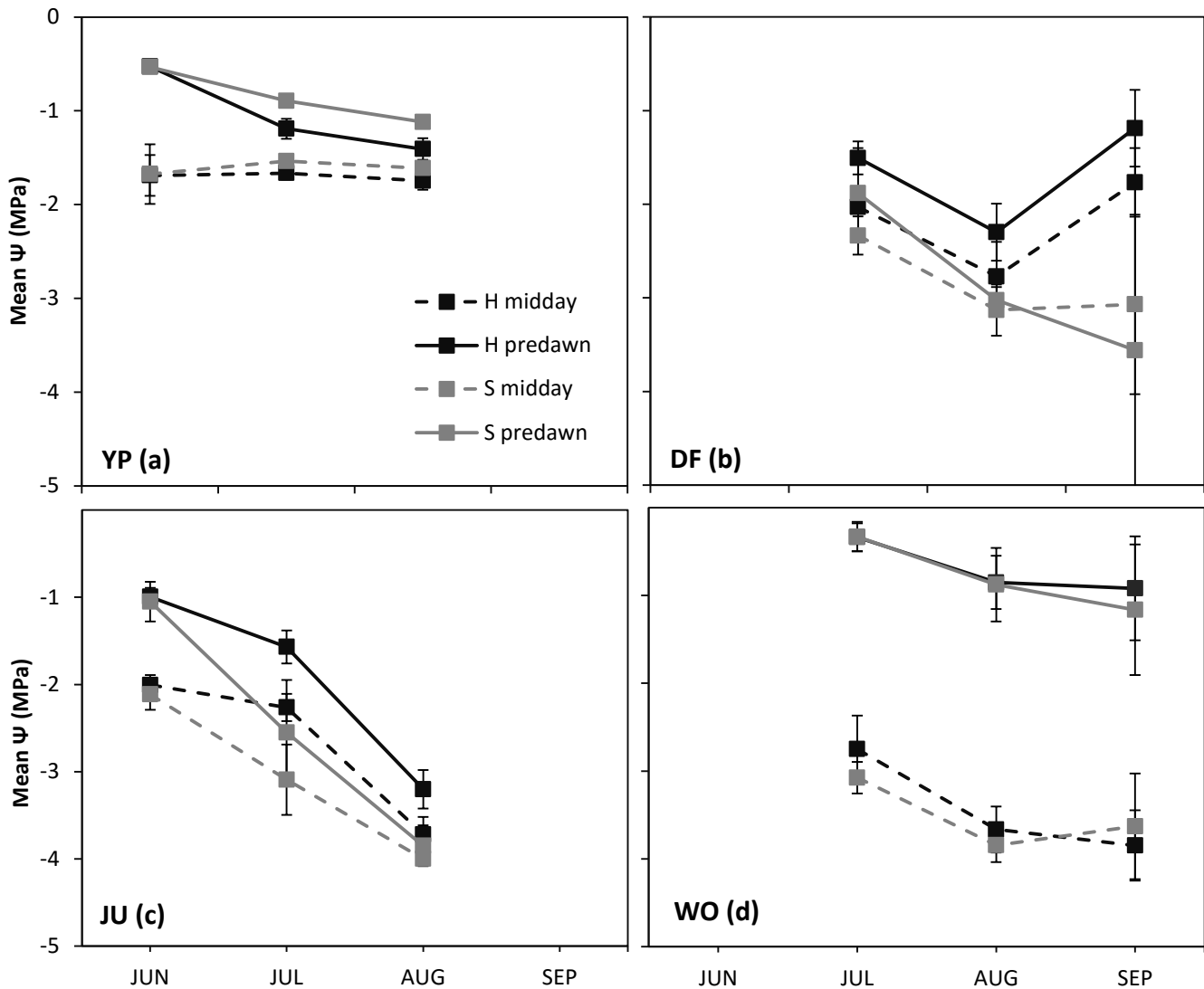


Figure 5. Mean predawn and midday leaf water potential for *stressed* (S) and *healthy* (H) trees at the four study sites. Error bars are standard deviation. DF= Douglas-fir, WO=white oak, JU=western juniper, YP=ponderosa pine.

To compare changes in Ψ at all sites during the summer, only the changes between July and August were statistically analysed. The largest declines in Ψ_{pd} and midday Ψ_{leaf} between July and August were seen at JU (Table 4; not significant $p>0.05$). It can be assumed that both Ψ_{pd} and midday Ψ_{leaf} of the *stressed* trees at JU were < -4 MPa in August since no water was observed exiting the twigs tested at pressures between 0 to -4 MPa but the pressure chamber could not measure below -4 MPa. If it had been possible

to record these measurements, it is likely that there would have been a significant difference in water potential between *healthy* and *stressed* trees in August.

At DF and WO, *healthy* and *stressed* trees showed significant declines in Ψ_{pd} and midday Ψ_{leaf} between July and August (Wilcoxon signed rank tests: $W=15$, $p=0.03$ in all cases; Table 4). Furthermore, DF was the only site where Ψ was significantly lower in *stressed* than *healthy* for individual monthly measurements, based on Wilcoxon signed rank tests. Differences were significant in July for midday Ψ_{leaf} and in July and August for Ψ_{pd} ($W=15$, $p=0.031$ in all cases). In September at the DF site, Ψ_{pd} of two *stressed* trees and one *healthy* tree were substantially lower (25-125%) than midday Ψ_{leaf} . These results were the opposite of what was expected - midday Ψ_{leaf} should always be lower than Ψ_{pd} because water-stress peaks in mid-afternoon, and Ψ_{pd} equilibrates with Ψ_{soil} when transpiration is negligible at night.

Table 4. Mean change in Ψ ($\Delta\Psi$; MPa) between July and August for *healthy* and *stressed* trees at each site $\pm 1SD$. *indicates significantly lower Ψ in August compared to July according to Wilcoxon signed rank test. DF= Douglas-fir, WO=white oak, JU=western juniper, YP=ponderosa pine.

Site	Sample time	<i>Healthy</i> mean $\Delta\Psi$	<i>Stressed</i> mean $\Delta\Psi$
DF	midday	-0.74* ± 0.36	-0.80* ± 0.23
DF	predawn	-0.79* ± 0.30	-1.14* ± 0.53
WO	midday	-0.92* ± 0.35	-0.77* ± 0.17
WO	predawn	-0.52* ± 0.30	-0.55* ± 0.32
JU	midday	-1.49 ± 0.04	-0.91 ± 0.40
JU	predawn	-1.67 ± 0.03	-1.30 ± 0.38
YP	midday	-0.10 ± 0.11	-0.08 ± 0.04
YP	predawn	-0.30 ± 0.21	-0.23 ± 0.04

In July and August, *stressed* trees at all sites (except YP) reached lower minimum Ψ_{pd} and midday Ψ_{leaf} than *healthy* trees (Table 5). DF was the only site where *stressed* trees had significantly lower minimum Ψ than *healthy* trees, and only for Ψ_{pd} (Wilcoxon signed rank test: $W=15$, $p=0.03$; Table 3). The DF site also showed the largest difference in minimum Ψ_{pd} and midday Ψ_{leaf} between *healthy* and *stressed* trees (up to 31% lower in *stressed* trees for Ψ_{pd}). At YP, *stressed* trees had higher minimum Ψ_{pd} and midday Ψ_{leaf} than *healthy* trees. In comparisons of all the monthly Ψ measurements, YP *stressed* trees

showed slightly higher Ψ (6-20%) than *healthy* trees, though this was never statistically significant (Table 13, Appendix).

Table 5. Mean minimum Ψ_{pd} and midday Ψ_{leaf} (MPa) of *healthy* and *stressed* trees at all sites $\pm 1SD$. * indicates significantly lower minimum Ψ in *stressed* trees compared to *healthy* trees according to a Wilcoxon signed rank test. DF= Douglas-fir, WO=white oak, JU=western juniper, YP=ponderosa pine.

Site	Minimum Ψ_{pd}		Minimum midday Ψ_{leaf}	
	<i>Healthy</i>	<i>Stressed</i>	<i>Healthy</i>	<i>Stressed</i>
DF	-2.30 \pm 0.30	-3.02* \pm 0.14	-2.77 \pm 0.37	-3.13 \pm 0.27
JU	-3.23 \pm 0.26	-3.85 \pm 0.23	-3.75 \pm 0.22	-4.00 \pm 0.00
WO	-0.85 \pm 0.30	-0.87 \pm 0.42	-3.67 \pm 0.26	-3.85 \pm 0.19
YP	-1.40 \pm 0.12	-1.12 \pm 0.06	-1.74 \pm 0.12	-1.61 \pm 0.09

Spearman’s rank correlations were performed to test for significant relationships between canopy loss and minimum Ψ_{pd} or midday Ψ_{leaf} at each site. There were negative relationships between canopy loss and minimum midday Ψ_{leaf} at every site except YP, yet the relationship was only significant at WO ($r_s=-0.656$, $n=10$, $p=0.043$). There were also negative relationships between canopy loss and minimum Ψ_{pd} at JU and DF, and positive relationships at YP and WO but none were significant. The lack of significant correlation between Ψ and canopy loss is due to the similar Ψ of all *stressed* trees despite large differences in the proportion of canopy lost. For JU, the correlation analysis was affected by the maximum range (0 to -4MPa) of the pressure chamber used for measurements which could not capture the minimum Ψ of some of the *stressed* trees which were <-4 MPa. At all sites, the tree with the lowest Ψ never had the largest canopy loss.

6.2 Tree-rings

The tree-ring chronologies showed considerable variation in age between sampling sites: DF had the youngest trees whilst JU had the oldest (Table 6). The trees from the JUS (*stressed* JU trees) chronology stopped producing growth rings after the 1950s, though all trees still had a small proportion of living foliage remaining when sampled in 2015. The JU chronologies showed the strongest common growth signal (high EPS and interseries

correlation; Table 6) which is likely a response to climate. The WOH (*healthy* WO trees) chronology had low EPS and interseries correlation and the two DF chronologies also had low interseries correlation values (Table 6) suggesting that trees within these chronologies exhibited different growth patterns and were not responding as strongly to climate. None of the chronologies had significant first order correlation.

Table 6. Descriptive statistics for the ring-width index (RWI) chronologies at each sampling site. EPS and mean interseries correlation are measures of the common growth signal expressed by the chronology. DFH=*healthy* Douglas-fir, DFS=*stressed* Douglas-fir, WOH=*healthy* white oak, WOS=*stressed* white oak, JUH=*healthy* western juniper and JUS=*stressed* western juniper.

Chronology	Mean RWI \pm 1SD	Earliest dateable ring	EPS	Mean interseries correlation	First order autocorrelation
DFH	0.996 \pm 0.168	1973	0.782	0.441	0.133
DFS	0.983 \pm 0.166	1978	0.659	0.264	0.288
WHO	0.985 \pm 0.137	1922	0.393	0.109	0.188
WOS	0.987 \pm 0.195	1922	0.621	0.268	-0.013
JUH	0.982 \pm 0.299	1883	0.908	0.597	0.049
JUS	0.978 \pm 0.333	1950	0.813	0.447	0.022

Chronologies were correlated to growing year (October-September) climate to investigate whether *stressed* and *healthy* chronologies at the sites showed any differences in climate sensitivity. For JU trees, the correlations were performed during a different time period (1933-1952) to the WO and DF chronologies (1995-2014) because JU *stressed* trees stopped producing growth rings after the 1950s. There were no significant differences in mean growing year air temperature or total precipitation at JU between 1933-1952 and 1995-2014 ($P > 0.05$), suggesting that any differences in the climate correlations between JU and the other sites were not due to differences in the time period used but rather due to site conditions and tree responsiveness to climate.

At JU, both *healthy* and *stressed* trees showed positive correlations with precipitation, indicating that radial growth was water-limited. The DF chronologies showed no significant correlations with the growing year climate variables (Table 7) but they did show significant correlations to monthly and seasonal climate variables (discussed below; Figure 6). WO was the only site to show slight differences in climatic sensitivity between *healthy* and *stressed* trees. The *healthy* trees showed significant negative correlation to all

three temperature variables tested whilst *stressed* trees only showed significant negative correlation to maximum temperature. The negative relationship to maximum temperature suggests that both *healthy* and *stressed* trees were temperature-limited. WOS was the only chronology to show significant correlation with climate from the previous growing year (precipitation: $\rho=0.52$, $P=0.02$). Given that none of the chronologies had statistically significant first order autocorrelation (Table 6) it is not surprising that they showed low correlation values with climate of the previous growing year.

Table 7. Results of Spearman’s rank correlations (ρ) between tree-ring chronologies and four climate variables averaged (temperature) or summed (precipitation) over the growing year (October – September). *indicates significant correlation ($p<0.05$). Time period of correlations is: 1995-2014 at DF and WO; 1933-1952 at JU. DFH=*healthy* Douglas-fir, DFS=*stressed* Douglas-fir, WOH=*healthy* white oak, WOS=*stressed* white oak, JUH=*healthy* western juniper and JUS=*stressed* western juniper.

Climate variable	DFH	DFS	WOH	WOS	JUH	JUS
Precipitation	0.34	0.32	0.35	0.38	0.50*	0.55*
Mean max temperature	-0.18	-0.10	-0.62*	-0.48*	-0.20	-0.18
Mean temperature	0.03	0.19	-0.58*	-0.35	-0.29	-0.23
Mean minimum temperature	0.15	0.35	-0.48*	-0.16	-0.32	-0.23

To further elucidate how the trees at the different sites responded to climate, Spearman’s rank correlations were repeated among tree-ring series and the same climate variables on monthly and seasonal time scales. Figure 6 shows the results of the monthly total precipitation and maximum air temperature since the trees showed the strongest response to these two variables (Table 7) and both are closely connected to drought. Seasonal correlations generally showed the same results as the monthly climate correlations.

DF showed the strongest positive response to precipitation in spring with no difference between *healthy* and *stressed* trees. In the seasonal correlations, *healthy* JU trees showed a significant, positive correlation to precipitation in the winter of the current growing year (correlation was also strong and positive for *stressed* trees during the same season). JU trees also showed a strong response to maximum temperature, with significant negative correlations during the winter of the current growing season for *healthy* and *stressed* trees (seen in both monthly and seasonal correlations). Significant negative correlation was also seen between maximum temperature and *stressed* tree growth in winter at WO.

These negative relationships to winter air temperatures are likely due to the influence of air temperature on whether precipitation falls as rain or snow, which can impact soil water availability later in the growing season. There were some individual months of significant correlation between DF tree growth and maximum temperature but this was not reflected in the seasonal correlations.

The tree-ring chronologies were also correlated against SPEI aggregated over different time periods to investigate how the trees responded to moisture availability at different times during the growing season and over multiple years (Table 8). It was expected that correlations between ring-width and SPEI would be positive since higher values of SPEI indicate a wetter climate. Indeed all significant correlations between the tree-rings and SPEI were positive.

None of the chronologies showed a significant relationship to SPEI aggregated over 72 months and only *stressed* trees at WO showed a very strong correlation to the 36 month SPEI, echoing the strong correlations between *stressed* WO trees and prior year precipitation. The *stressed* trees at DF were the only ones to show significant correlation to the summer SPEI. These results confirm the monthly climate correlations (Figure 6) which showed a strong response of DF trees to precipitation between March and July. At JU both *healthy* and *stressed* trees showed the same response, with significant correlations to the 12 month and winter SPEI. These results reflect the strong positive correlation of the chronologies to precipitation over the whole growing year (Table 7) and seasonal correlation to winter precipitation.

PRECIPITATION

MAXIMUM AIR TEMPERATURE

— Healthy - - - Stressed
 ■ Stressed P<0.05 ▲ Healthy P<0.05

— Healthy - - - Stressed
 ■ Stressed P<0.05 ▲ Healthy P<0.05

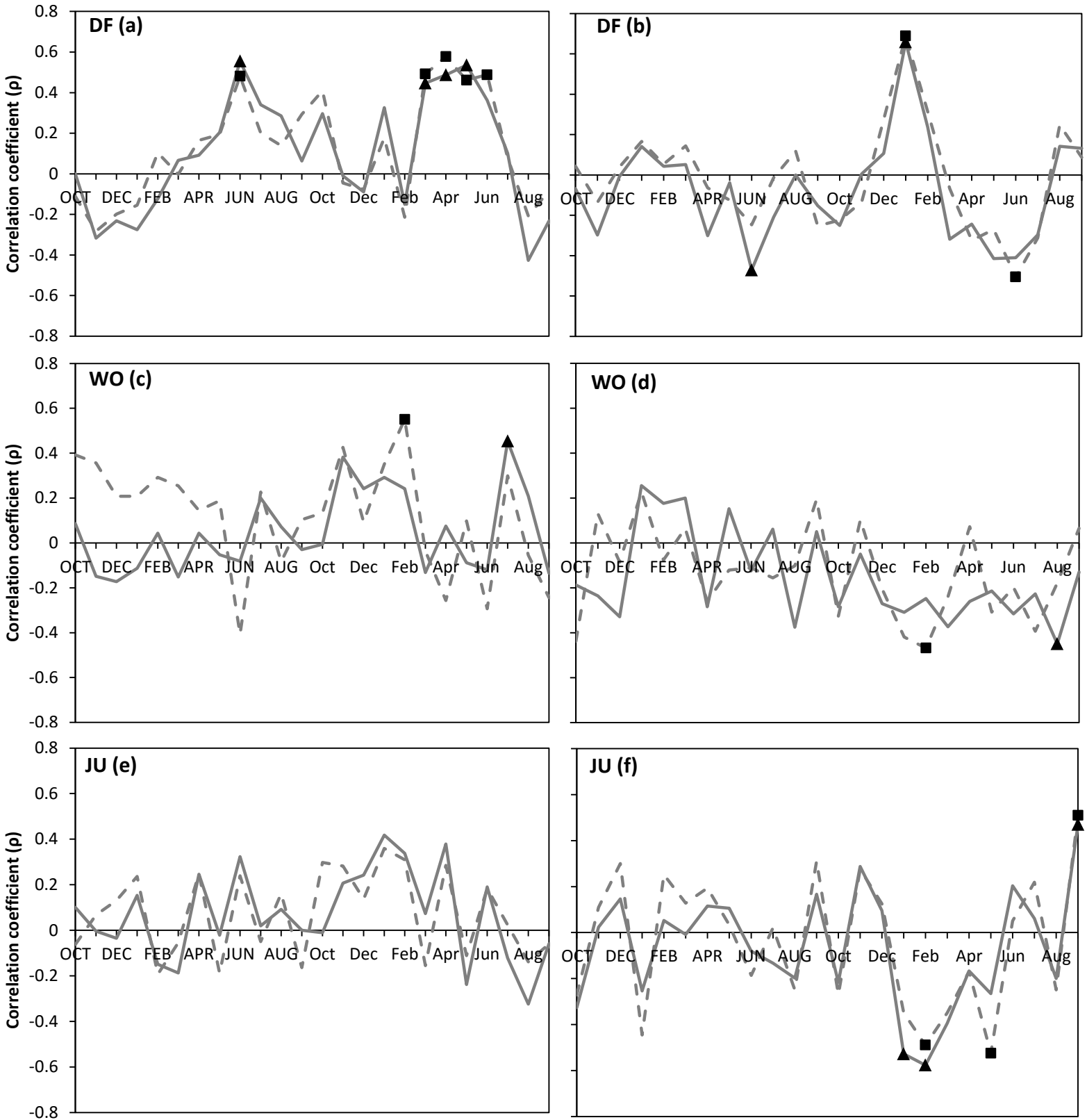


Figure 6. Average monthly Spearman's rank correlations of tree-ring series and precipitation (left) or max air temperature (right). Solid line = *healthy* tree average, dashed line = *stressed* tree average. Months in capital letters are correlations between ring width (current year) and climate from the prior growing year. Solid black triangles (*healthy* trees) or squares (*stressed* trees) indicate significant correlation ($p < 0.05$). Time period of correlations is: 1995-2014 at DF and WO; 1933-1952 at JU. DF=Douglas-fir, WO=white oak and JU=western juniper

Table 8. Spearman’s rank correlations between chronologies from *healthy* and *stressed* trees at each site and SPEI aggregated over different length time periods. All SPEI periods were computed following the growing year (October-September). “6 months winter” SPEI is October-March, and “6 months summer” SPEI is April-September. *indicates significant correlation ($p < 0.05$). Time period of correlations is: 1995-2014 at DF and WO; 1933-1952 at JU. DFH=*healthy* Douglas-fir, DFS=*stressed* Douglas-fir, WOH=*healthy* white oak, WOS=*stressed* white oak, JUH=*healthy* western juniper and JUS=*stressed* western juniper.

SPEI	DFH	DFS	WOH	WOS	JUH	JUS
72 months	-0.19	-0.16	-0.27	0.32	0.09	0.19
36 months	-0.08	-0.04	0.07	0.70*	0.32	0.41
12 months	0.40	0.35	0.48*	0.40	0.49*	0.58*
6 months winter	0.22	0.14	0.44	0.49*	0.56*	0.58*
6 months summer	0.40	0.62*	-0.05	-0.26	-0.03	0.10

Table 9. Mean basal area increment (BAI) and Gini index (G) for *healthy* and *stressed* trees at each site ± 1 SD. Time span is the longest time period common to all trees at each site over which the BAI and G were calculated. *indicates significantly lower BAI or significantly higher Gini in *stressed* trees compared to *healthy* trees at a site. DFH=*healthy* Douglas-fir, DFS=*stressed* Douglas-fir, WOH=*healthy* white oak, WOS=*stressed* white oak, JUH=*healthy* western juniper and JUS=*stressed* western juniper.

Growth variable	DFH	DFS	WOH	WOS	JUH	JUS
Time span	1994-2014		1976-2014		1933-1952	
Mean BAI (mm ² /yr)	1682 ± 812	1795 ± 812	1060 ± 592	1395 ± 775	673 ± 462	475.5 ± 273
Mean G	0.115 ± 0.024	0.106 ± 0.038	0.110 ± 0.040	0.141 ± 0.022	0.144* ± 0.025	0.210* ± 0.031

BAI and G were calculated for individual tree-ring series (Table 9) and used to test for significant differences in tree growth rate and variability, respectively, between *healthy* and *stressed* trees at each site. The highest rates of tree growth were occurring at DF and the lowest at JU, but all trees showed large interannual variability in growth (large standard deviation of BAI; Table 9). Paired t-tests showed that the BAI of *healthy* trees was not significantly greater than *stressed* trees at any of the sites ($p > 0.05$). However, the same test performed on each year between 1995-2014 (Table 10) showed that WO *stressed* trees had significantly lower growth ($p > 0.05$) than their *healthy* counterparts between 2010-2013. Paired t-tests also showed that the G of *healthy* trees was significantly lower than that of *stressed* trees at JU ($t = -5.12$, $p = 0.003$) indicating that *healthy* trees had less interannual variability in their growth than their *stressed* counterparts (Table 9).

SEA was performed to test the tree-ring chronologies for significant divergences from mean growth rate during and following severe drought years. The SEA showed no significant results at DF but similar results at WO and JU (Figure 7). At both WO and JU, the *stressed* trees showed significantly lower growth during a drought year whereas no significant change in growth was observed in the *healthy* trees. At WO, tree growth for both *healthy* and *stressed* trees remained low for two years following severe drought whereas at JU growth recovered quicker. *Stressed* trees at DF were the only ones to show a positive growth response during a severe drought, although these results were not significant.

Table 10. Normalized BAI for 20 years before 2015. * indicates *stressed* trees have significantly lower mean normalized BAI compared to *healthy* trees based on Wilcoxon signed rank test. † indicates severe drought year (growing year 12 month SPEI <-1). DFH=*healthy* Douglas-fir, DFS=*stressed* Douglas-fir, WOH=*healthy* white oak, WOS=*stressed* white oak.

Year	DFH	DFS	WOH	WOS
2014†	-1.28	-0.58	0.38	-0.32
2013	-0.38	0.26	0.12	-0.59*
2012	0.98	0.66	0.60	0.06*
2011	1.38	1.20	0.86	-0.14*
2010	1.50	0.87	0.86	-0.28*
2009†	0.15	-0.05	0.81	-0.04
2008	-0.48	-0.52	1.12	1.37
2007	-0.52	-0.80	1.10	0.69
2006	0.61	0.21	0.08	-0.09
2005†	0.43	1.22	-0.25	-0.69
2004	-0.52	-0.22	-0.24	0.12
2003	0.01	0.21	-1.02	-1.63
2002	-0.03	-0.01	-0.43	-0.55
2001†	-0.35	0.30	-0.35	-0.46
2000	-0.15	-0.40	-0.29	0.58
1999	-0.62	-0.40	-0.30	1.99
1998	-0.15	-0.15	-0.84	0.28
1997	-0.24	-0.37	-0.85	0.03
1996	-0.05	-0.61	-0.66	0.14
1995	-0.26	-0.84	-0.67	-0.49

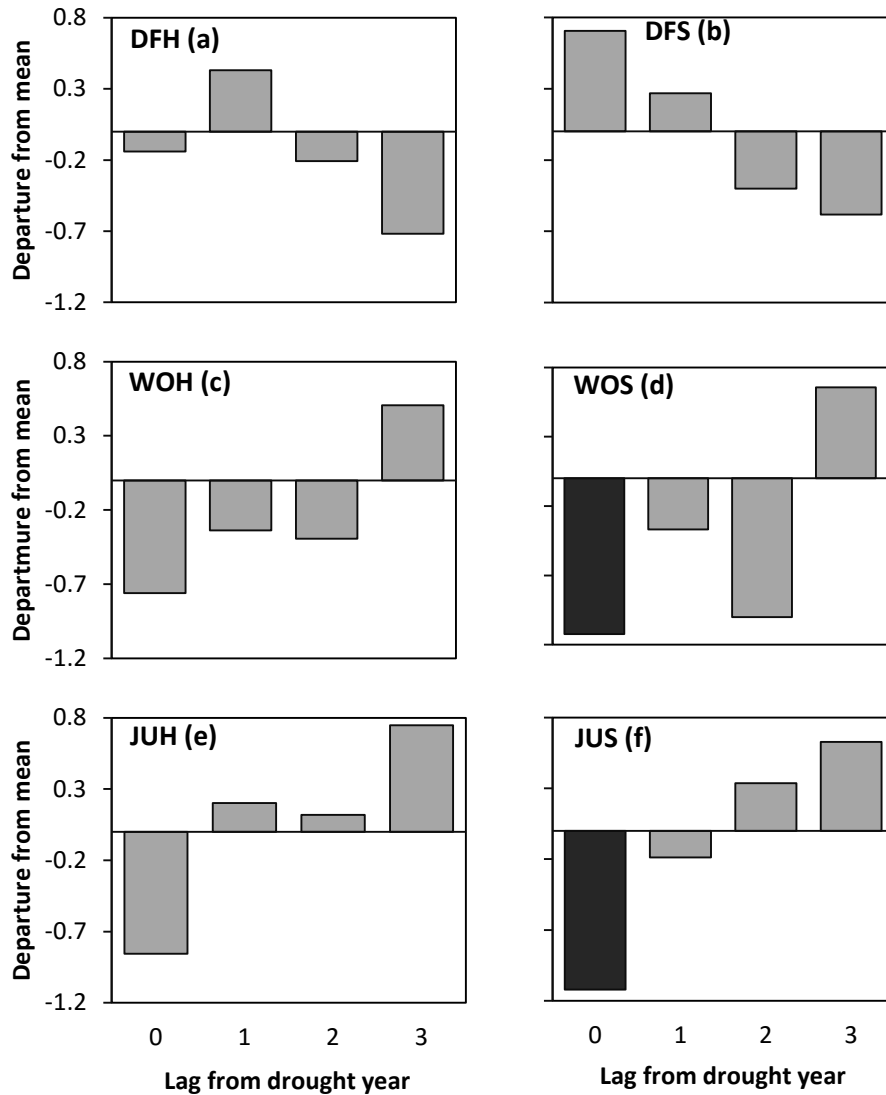


Figure 7. Superposed Epoch Analysis (SEA) using the three worst drought years during time period of analysis based on 12 month growing year SPEI. SEA was performed for 0 to 3 years after a drought year (where year 0 = drought year). Values are normalized departures from mean growth. Dark grey bars are significant ($p \leq 0.05$). Time periods of analysis are: 1994-2014 (DF), 1976-2014 (WO), 1933-1952 (JU) which represented the period common to all trees at each site. At DF drought years are: 1994, 2001 and 2005. At WO drought years are: 1977, 2001 and 2005. At JU drought years are: 1934, 1939 and 1949. DFH= *healthy* Douglas-fir, DFS= *stressed* Douglas-fir, WOH=*healthy* white oak, WOS=*stressed* white oak, JUH=*healthy* western juniper and JUS=*stressed* western juniper.

7. DISCUSSION

Hypothesis 1: Summer 2015 weather conditions were hotter and drier compared to 1981-2010 normals which led to significant reductions in tree leaf and soil water potential.

7.1 Climatic conditions

Droughts are not unusual in Oregon, particularly east of the Cascades during the hot and dry summer months (OCCRI 2010). However, comparisons of 2015 weather data with a 30 year baseline period indicated that the 2015 summer and preceding winter conditions were exceptionally warm and dry. The warm winter conditions led to an unusually low snowpack (USDA 2015). In this region, precipitation mainly falls during winter and spring (OCCRI 2010) so the winter drought conditions would have exacerbated summer drought by preventing adequate soil water recharge which plants in this ecosystem are highly dependent on (Thomas et al. 2009). In the summer, the combination of raised air temperatures and reduced precipitation would not only have limited soil water availability but also increased rates of transpiration and evaporation, further worsening soil water depletion. The summer 2015 drought was most severe at the sites east of the Cascades, perhaps due to the rainshadow effect of the mountains.

The drought conditions prior to and during the summer 2015 may be linked to “The Blob”: warm sea-surface temperature anomalies occurring in the northeastern Pacific Ocean since the winter 2013-2014 (Floyd 2015). “The Blob” was caused by high sea level pressures and low winds which combined to reduce ocean surface heat loss and vertical mixing (Bond et al. 2015). The drought may also be connected to the Pacific Decadal Oscillation (PDO) which has been moving into a warm phase since 2014 (NOAA 2016). Sea surface temperatures in the Pacific are strongly linked to western US air temperatures and the warm phase of the PDO is often associated with drought conditions in central Oregon (Thomas et al. 2009).

7.2 Comparing Ψ measurements to expected values

Comparisons to literature values can only provide a rough estimate of the decline in Ψ during the summer 2015 drought since the literature values were collected at different sites with different soil and tree characteristics to those measured here. In addition, differences in the size of tree organs (e.g. leaves, twigs or small branches) used for Ψ measurements in the literature, which have different Ψ ranges (Meinzer et al. 2010), introduces discrepancies in comparisons to literature values. Furthermore, it was difficult to assess whether the values reported truly represented ‘pre-drought’ conditions and a range of values may have been reported.

Nevertheless, it appears that soil water availability (based on Ψ_{pd} as a rough proxy measurement) was severely limited during summer 2015 at all sites compared to “pre-drought” values due to the exceptional drought conditions (Table 11). No “pre-drought” values for white oak were reported in the literature. Phillips et al. 2003a however recorded -0.9 MPa as their minimum Ψ_{pd} in summer 1999 which was similar to the -0.86 MPa value from this study (with both summers having similar amounts of summer precipitation). Furthermore, measurements by Law and Waring (1994) at sites close to the ones used in this thesis found minimum Ψ_{pd} of -2 MPa and -2.8 MPa during the summer of 1990 for Douglas-fir and western juniper respectively. These values are higher than the values measured here (Table 11), probably due to the fact that nearly twice as much precipitation fell during the summer 1990 compared to the summer 2015. Measured Ψ_{min} were also lower than reported “pre-drought” values, though the decline between pre- and peak-drought conditions was smaller than for Ψ_{pd} . The large declines in Ψ_{pd} and midday Ψ_{leaf} over the course of the summer (particularly at DF and WO) indicate that the trees were responding to the sustained drought conditions over the summer which did not improve until mid-September.

Although trees at all the sites had lower Ψ than ‘pre-drought’ literature values, they exhibited similar Ψ_{min} to those recorded in the literature (Table 11). Thus although summer drought conditions were severe, they did not cause exceptional drops in Ψ . DF was the only site where trees (one *healthy* and three *stressed*) reached Ψ_{min} lower than

minimum values reported in the literature ($<3\text{MPa}$). These trees were unable to maintain isohydric control of their leaf water potential, probably as a result of severe loss of hydraulic conductivity and lack of carbon assimilation. In two of the *stressed* trees, water potentials did not recover during the September round of measurements, indicating long-term damage to their hydraulic system which could ultimately lead to mortality. At YP however, despite more severe drought conditions, both *stressed* and *healthy* trees maintained isohydric control of their Ψ_{leaf} , demonstrating that ponderosa pine exerts stronger stomatal control compared to Douglas-fir (Johnson et al. 2009). At both JU and WO, trees showed declines in midday Ψ_{leaf} that paralleled declines in soil water potential, supporting the theory that both species were anisohydric (Meinzer et al. 2013; McDowell et al. 2008b; West et al. 2008).

Nevertheless, all species (both *healthy* and *stressed* trees) experienced a degree of drought stress since they reached either the point of stomatal closure and/or Ψ_{50} threshold for at least one month during the summer period (Tables 11 and 12). The reductions in hydraulic conductance and carbon assimilation were most significant at the DF site which exhibited the most negative safety margin and experienced stomatal closure at the same time (Table 12). The effects of the summer drought were least severe at JU and WO (Table 12). But, it is also typical for these species to lose a large proportion of their hydraulic conductance during normal summer drought conditions in Oregon (Law and Waring 2015). Without continuous long-term measurements of stomatal conductance, photosynthesis and Ψ at the four sites themselves, it is difficult to assess the severity of the drought stress experienced by the trees during summer 2015. Based on these results, hypothesis 1 can be accepted in terms of the trees showing significant reductions in Ψ compared to literature “pre-drought” values (and for DF and WO which showed significant reductions in Ψ over the course of the summer) but not in terms of the trees showing significant reductions in Ψ compared to average Ψ_{min} values.

7.3 Severe drought stress response at DF

All the DF trees experienced severe loss of hydraulic conductivity and, presumably, reductions in the rate of carbon assimilation during the summer. Nevertheless, Johnson et

al. (2012b) argue that frequent embolisms are part of the hydraulic strategy of many conifer species. By allowing embolisms to occur in needles and fine roots, which can be “easily” repaired, trees are protected from more substantial damage to stem water transport. Indeed experiments have shown that Douglas-firs have daily cycles of embolisms in shoots around midday and subsequent repair in the afternoon and evening, even during non-drought conditions (Woodruff et al. 2007; Johnson et al. 2009).

However, by August, all trees at the DF site had Ψ_{pd} values lower than the Ψ_{50} and stomatal closure threshold. It can be speculated therefore that trees may have been unable to repair leaf embolisms overnight. Or even if embolism repair were occurring, “cavitation fatigue” due to repeated embolisms and very low Ψ may have weakened the tree xylem and made it more vulnerable to future embolisms (Hacke et al. 2001). For most DF trees, Ψ recovered during September, but for two of the *stressed* trees, they continued to decline. This may indicate that these trees suffered long-term hydraulic damage and were not able to repair needle embolisms or alternatively that they could not recover from the carbon starvation caused by significant needle shedding (e.g. Galiano et al. 2011). Kane et al. (2014) noted that Douglas-fir mortality lagged drought events by ~3 years and were strongly associated with beetle attack. Signs of bark beetle were present on other trees at the DF site (not on the trees measured here), and drought stress can render trees more vulnerable to attack (Kane et al. 2014). The severe drought stress experienced by these *stressed* trees could predispose them to beetle attack which, along with sustained drought conditions, could likely kill these trees within the next few years.

Table 11. Literature and measured Ψ values. Literature “pre-drought” values are averages of reported Ψ without drought stress (usually measured in spring). Measured minimum values are averages of the minimum values of *healthy* and *stressed* trees. DF=Douglas-fir, WO=white oak and JU=western juniper and YP=ponderosa pine.

Species	Predawn Ψ (MPa)		Midday Ψ (MPa)			Literature Ψ value corresponding to stomatal closure (MPa)	References
	Literature “pre-drought”	Measured minimum	Literature “pre-drought”	Literature minimum	Measured minimum		
DF	-0.55	-2.66	-1.36	-3.0	-2.95	-2.0	Law 1993; Warren et al. 2004; Woodruff et al. 2007
JU	-0.5	-3.54	-1.8	-5.5	-3.88	-3.0	Miller 1990; Law 1993
WO		-0.86		-4.4	-3.76		Johnson et al. 2009
YP	-0.35	-1.26	-1.05	-1.89	-1.45	-2.1	Ruehr et al. 2014; Ryan et al. 2000; Choat et al. 2012; Hubbard et al. 2001

Table 12. Literature values of Ψ_{50} (Ψ corresponding to 50% loss of conductivity) compared to average measured minimum midday Ψ_{leaf} for *healthy* and *stressed* trees for each site. DF=Douglas-fir, WO=white oak and JU=western juniper and YP=ponderosa pine.

Species	Literature Ψ_{50} (MPa)	Safety margin (minimum midday $\Psi - \Psi_{50}$; MPa)		References
		<i>Healthy</i>	<i>Stressed</i>	
DF	-1.35	-1.42	-1.78	Johnson et al. 2009
JU	-9.0	5.25	5	Willson et al. 2008
WO	-3.61	-0.06	-0.24	Johnson et al. 2012a
YP	-1.62	-0.12	0.01	Johnson et al. 2012a

Hypothesis 2: Trees with greater drought-induced foliage loss suffered greater drought stress compared to trees with little foliage loss during the summer 2015.

7.4 The relationship between foliage loss and Ψ

Plants respond to drought through structural and physiological adjustments (van der Molen et al. 2011). Examining the relationship between foliage loss (structure) and Ψ (physiology) is an attempt to connect both processes. The correlation results suggested there was little relation between foliage loss and drought stress in trees. At DF, WO and JU, *stressed* trees did reach lower minimum Ψ_{pd} and Ψ_{min} , and had smaller or more negative safety margins than *healthy* trees, as expected, but these results were only statistically significant at DF (Tables 5 and 12). This may be partly due to the small sample sizes (and large standard deviations of measurements in some cases) which required a large difference in Ψ between *healthy* and *stressed* trees in order to produce significant results. Furthermore, differences in Ψ and foliage loss between *healthy* and *stressed* trees may have been caused by different factors for each of the species analysed. Since there is not a clear, significant difference in the level of drought stress experienced by *healthy* and *stressed* trees for most species (except DF) the second hypothesis cannot be accepted.

At YP, *stressed* trees had similar Ψ_{pd} and midday Ψ_{leaf} values to *healthy* trees despite significant (up to 85%) canopy loss. It is important to consider that at the YP site and in the local vicinity there was only one other *stressed* tree (already dead) apart from the two *stressed* trees measured here. At the other sites, trees with abnormal foliage loss were more common. Given the homogeneity of site conditions and tree characteristics at the YP site (a plantation), it would be expected that drought-induced needle shedding would be more widespread if the whole site was affected by drought. It is possible that the *stressed* trees had shed needles due to beetle or pathogen attack, which is more likely to occur when trees are drought stressed (Bréda et al. 2006). When cored, wood from the other dead tree at the site was discoloured, suggesting the presence of a fungus such as *Ceratocystic minor*, a blue-staining pathogenic fungus associated with the western pine

beetle (Paine 1984). However, apart from needle loss and discolouration, the two *stressed* trees measured showed no signs of beetle attack (USDA 1974).

The similarity of midday Ψ_{leaf} and Ψ_{pd} between *healthy* and *stressed* trees at YP is likely due to the fact that ponderosa pine is strongly isohydric. Hubbard et al. (2001) found that it was only at an extreme 99% reduction in stem hydraulic conductivity that Ψ_{leaf} of ponderosa pine seedlings declined below their isohydric threshold value to -2.1 MPa. Since ponderosa pine is able to maintain such strong isohydric control of leaf water potential, measuring stomatal conductance or transpiration may have been a more informative way of examining the relationship between foliage loss and drought stress.

WO was the site with the smallest difference in Ψ between *healthy* and *stressed* trees but the only site to show significant negative correlation between midday Ψ_{leaf} and foliage loss. Thus the lower the midday Ψ_{leaf} , the more foliage was shed, suggesting that foliage loss was a successful drought adaptation by *stressed* trees to maintain their Ψ at sustainable levels similar to *healthy* trees. Oaks are known to shed leaves prematurely during drought (Abrams 1990; Suarez et al. 2004). Leaf shedding reduces the leaf area to sapwood area ratio, thus increasing stem water supply per area of leaf and preventing unsustainable declines in midday Ψ_{leaf} (Bréda et al. 2006). Leaves also have high metabolic costs so shedding them may reduce C demand, compensating somewhat for the loss in C assimilation due to shedding or declines in stomatal conductance (Sala et al. 2010). Furthermore, WO leaves were browning prematurely, indicating that trees were able to withdraw valuable nutrients from them before shedding (rather than green leaf shedding which may be a symbol of leaf embolism; Bréda et al. 2006). It appears that *stressed* and *healthy* oaks were facing similar soil water stress since both sets of trees had similar Ψ_{pd} . Therefore, other factors such as small differences in tree genetics, location (affecting exposure to sunlight and wind and thus rates of evapotranspiration and photosynthesis) and competition with surrounding trees may have disadvantaged or exacerbated drought conditions for *stressed* trees compared to *healthy* trees. Indeed, white oaks are very strongly affected by competition from surrounding trees (Gould et al. 2011).

At DF and JU, *stressed* trees usually had lower Ψ_{pd} and midday Ψ_{leaf} compared to *healthy* trees. It may be the case that the lower midday Ψ_{leaf} in *stressed* trees were a result of *stressed* trees experiencing greater soil water stress (seen as lower Ψ_{pd}) than *healthy* trees. Perhaps foliage loss in *stressed* trees did not reduce transpiration enough to prevent midday Ψ_{leaf} of *stressed* trees from declining below those of *healthy* trees. This may be the case for DF *stressed* trees which experienced the least foliage loss of all the species examined, but not for JU *stressed* trees which had the highest average canopy loss. There may be a threshold level of foliage loss that must be reached in order for transpiration or stomatal conductance to be significantly reduced (and for Ψ to recover) which likely differs among species. For instance Pataki et al. 1998 showed that it was only after 55% removal of foliage from loblolly pine that transpiration and conductance declined significantly and Miller 1990 found no significant change in the same parameters for western juniper after removal of 50% of foliage. However these experiments did not occur during plant drought stress which likely affects the relationship between the proportion of foliage lost and transpiration or conductance since there is a greater need to conserve water relative to carbon assimilation.

The interpretation of the relationship between leaf shedding and Ψ is complicated by not knowing when leaf shedding began at the sites and how it progressed during the summer. This made it difficult to interpret whether leaf shedding was a result of low Ψ , and whether leaf shedding was followed by a recovery of Ψ_{leaf} . It is also possible that tree canopy area had already been substantially reduced during previous droughts. From personal observations it appeared that leaf shedding at DF and WO was a recent phenomenon beginning in the late spring or summer 2015. At JU however, it did not appear that foliage loss was a recent occurrence. This observation could be supported by the tree-ring dating of the *stressed* trees around the JU site which stopped producing growth rings (at DBH) between 1956-2007. This suggests that not enough carbon was assimilated to produce complete growth rings, potentially due to a reduction in leaf area. Indeed, at JU loss of needles could be a long-term drought adaptation by *stressed* trees to maintain their Ψ at sustainable levels. For example, Suarez et al. 2004 found that trees

with leaf area reductions due to a prior drought were more likely to survive future droughts than those with no prior leaf area reduction.

7.5 Water potential: methodological issues

Due to the time and resource intensiveness of Ψ measurements, as well as the large number of species examined, only small sample sizes could be used. Inconsistencies during measurement (which were unavoidable in some cases) also introduced inconsistencies in the Ψ data. For example, at the eastern sites (JU and YP) the canopy was easily accessed by ladder allowing for quick sample excision and transferal to the pressure chamber whereas at the western sites (DO and WO), an arborist slingshot had to be used to excise samples. Thus at the western sites, samples were not all from the same branch (so were not experiencing exactly the same growing conditions) and there was a longer time period (a couple of minutes at most) between the sample being excised from the tree and placed in the pressure chamber, which could cause these measurements to be slightly lower than the true value (Turner 1981). These difficulties may partially explain why the data from DF and WO have larger standard deviations than at the other two sites.

In a few cases, trees at the DF site had lower Ψ_{pd} compared to midday Ψ_{leaf} which is highly unexpected. This may be due to the sampling technique used which meant that it was difficult to tell whether samples gathered were from twigs that had just been excised from the tree or if they had been excised earlier. Nevertheless, results were consistent even on samples from different branches for the same tree. It is also possible that nocturnal transpiration was occurring, causing Ψ_{pd} to remain low (Kavanagh et al. 2007). However it would be surprising if sufficient nocturnal transpiration were occurring to cause Ψ_{pd} to be much so lower than midday Ψ_{leaf} .

At the eastern sites, samples could be covered with a plastic bag wrapped in reflective aluminium foil to allow leaf and stem Ψ to equilibrate (Choat et al. 2012) prior to picking but this was not possible at the western sites. Therefore the Ψ values at the eastern sites represent stem xylem Ψ whereas at the western sites they are leaf Ψ (Choat et al. 2012). In addition, at DF, WO and JU it was not possible to sample individual needles or leaves

therefore small twigs were measured, whereas at YP individual needle fascicles could be measured. Since there are small differences between xylem and leaf Ψ , these will be reflected in the Ψ measurements at the four sites. The Ψ measurements were also carried out by different people which could lead to further discrepancies in the results. However, since the same sampling technique was consistently used at each site, these discrepancies should have little influence on the final conclusions of this thesis.

Hypothesis 3: Trees with greater foliage loss experienced lower rates of growth, more variable growth and responded more sensitively to climate prior to 2015 compared to trees with little foliage lost.

7.6 The response of tree growth to climate

Analysing the relationship of tree growth to drought-related climate variables can help elucidate the physiological response of the trees to the summer 2015 drought. JU chronologies showed the strongest response to annual precipitation, which was expected since JU was the most water-limited ecosystem (Berner and Law 2015). Trees at DF responded positively to spring-time precipitation, following previous findings that Douglas-fir stemwood growth is highly dependent on winter and spring precipitation and is limited after the onset of summer drought (Park Williams et al. 2013; Beedlow et al. 2013). WO trees were more sensitive to air temperature than precipitation, suggesting that they were not as water-limited as the other two species. Since many oak species are drought-tolerant due to their many morphological and physiological adaptations to drought (Abrams 1990) this is not surprising. Therefore the combination of high air temperatures and limited precipitation during the 2015 drought and in the year prior would have affected all three species.

Stressed and *healthy* trees at each site showed slight differences in their response to climatic variables, all suggesting that *stressed* trees were more sensitive to drought. Therefore the part of hypothesis 3 relating to climate sensitivity differences between *healthy* and *stressed* trees can be accepted. At WO, only *stressed* WO trees were significantly correlated to previous year precipitation and 36 month SPEI. This suggests

that the *stressed* trees had a more lagged or longer-term response to water availability than their *healthy* counterparts. It could be because *stressed* trees are more reliant on stored carbohydrates which accumulate during prior growth years (and therefore may be affected by prior precipitation and long-term drought conditions) than *healthy* trees, perhaps due to less favourable growing conditions. Therefore the *stressed* trees may have been more sensitive to the low precipitation during 2014 due to the drought, thus predisposing them to more severe drought-stress during 2015 compared to *healthy* trees. The SEA results also showed significant reductions in tree growth during a severe drought year for *stressed* but not for *healthy* WO trees, suggesting that overall *stressed* trees were more sensitive to drought. *Healthy* and *stressed* trees displayed no differences in Ψ_{pd} so differing sensitivities to drought events were not due to differences in soil water availability. Instead they may be related to differences in water use during growth (e.g. due to differences in hydraulic conductance or stem water storage; Phillips et al. 2003b) or due to differences in aspect and micrometeorology that cause *stressed* trees to be more heat-stressed or experience higher winds causing higher rates of transpiration.

At DF, only the *stressed* trees were significantly correlated to the summer 6 month SPEI. *Stressed* trees may have been more sensitive to summer droughts and therefore more vulnerable to drought-stress during the 2015 drought than *healthy* trees at the site. Since *healthy* and *stressed* trees showed differences in Ψ_{pd} , sensitivity to summer drought may have been related to differences in rooting patterns and ability to access soil water reserves which is particularly important during the hot and dry summer months (Bréda et al. 2006).

At JU, although *healthy* and *stressed* trees had similar correlations to climate variables and SPEI, only JU *stressed* trees showed a severe decline in growth during drought years. This is likely linked to the faster decline in Ψ_{pd} observed in *stressed* trees during the summer than *healthy* trees, due to faster use or more limited availability of soil water reserves. This could be due to differences in rooting which affects accessibility to soil water as well as soil properties, microtopography and aspect which affect soil water evaporation and amount of available soil water (Bréda et al. 2006). *Stressed* trees also

had lower midday Ψ_{leaf} than *healthy* trees, suggesting they controlled stomatal conductance less tightly, and thus may have had slightly higher rates of transpiration, leading to faster draw down of soil water reserves (although differences in leaf area may have negated differences in rate of transpiration at the tree level).

7.7 The relationship between foliage loss and tree growth

The results showed no definitive patterns in the relationships between foliage loss and tree growth or growth variability across the three species examined, therefore the parts of hypothesis 3 relating to tree growth and growth variability cannot be accepted. JU was the only site where *stressed* trees had significantly higher growth variability than *healthy* trees. Higher variability in growth is usually a sign of higher sensitivity to climate and/or disturbances which has been associated with increased likelihood of drought-related mortality (Ogle et al. 2000; Suarez et al. 2004). Indeed as discussed above, JU *stressed* trees did show larger declines in growth during drought years than *healthy* trees.

As for growth rate, there were no long-term differences between *stressed* and *healthy* chronologies at any of the sites. Nevertheless, WO *stressed* trees did show significantly lower growth than *healthy* trees for a few years prior to 2015. Some studies have associated slower growth rates with vulnerability to drought-related mortality, in part because slower growing trees take a longer time to recover from the effects of prior droughts or disturbances (Pedersen 1998; Suarez et al. 2004). At WO, severe droughts occurred in 2001, 2005, 2009 and 2014 and in each case, *stressed* trees showed reduced growth compared to *healthy* trees. This perhaps left *stressed* trees unable to successfully recover after the 2009 drought, especially given their heightened sensitivity to drought. It seems therefore that the *stressed* WO were predisposed to be more drought-stressed in 2015 compared to the *healthy* trees. Pedersen 1998 noted that oak trees died on average two decades after a major stress event that caused significant growth rate declines. Thus if *stressed* WO trees continue to experience significant reductions in growth due to recurring drought events, they may die within the next two decades.

Stressed Douglas-fir trees on the other hand exhibited smaller (though not significant) declines in growth during the aforementioned drought years compared to *healthy* trees. Work by Doughty et al. 2015 has shown that trees may prioritize stem growth during drought so as to maintain a competitive advantage, which may be the strategy employed by *stressed* Douglas-fir trees, particularly because they are young and densely planted. Doughty et al. 2015 note that trees maintaining high growth rates during drought were more likely to die in the following years because they did not prioritize root growth or repair. Since Douglas-firs are reliant on repairing frequent needle embolisms as part of their hydraulic strategy (Woodruff et al. 2007; Johnson et al. 2009), attempts to prioritize stem growth may explain why some Douglas-firs experienced such severe drought-stress.

In terms of future tree growth, premature needle shedding during summer 2015 may have a greater metabolic cost for evergreen needle trees compared to deciduous angiosperms like white oak. For ponderosa pine, Douglas-fir and western juniper, needle longevity is roughly 4.5, 5.5 and 5.6 years respectively (Berner and Law 2016). Evergreen needle trees (particularly from xeric ecosystems) may face higher metabolic costs for producing foliage than deciduous trees (Villar and Merino 2001), therefore replacing needles lost during drought may take longer, especially given that carbon reserves are already depleted. Carnicer et al. (2011) showed that Mediterranean forests in Europe never fully recovered their leaf area after defoliation following drought in the early 1990s. In addition, it has been observed that evergreen species are less efficient at translocating nutrients from senescing leaves than deciduous species, indicating further loss of resources during a drought period (Del Arco et al. 1991). Therefore the *stressed* trees at DF, YP and JU may be disadvantaged in the future compared to *healthy* trees, as they try to recover their leaf area, potentially leading to long-term declines in growth. *Stressed* WO trees are also likely to be disadvantaged in future since premature leaf shedding would have led to less carbohydrate accumulation and storage (Bréda et al. 2006) and thus fewer reserves to repair damage and contribute to growth in the following years.

7.8 Tree-rings: methodological issues

The main issues surrounding the processing of the tree-ring data related to the small sample sizes and the difficulties of dating the samples. It is recommended to sample at least 30 trees to have a robust sample size for use in dendrochronology (Speer 2010), but in this case chronologies were constructed from 5 trees. Furthermore, the lack of master chronologies for the DF and WO sites, coupled with the relatively young age of the trees and the difficulty of spotting clear annual rings in ring-porous white oak made dating these chronologies difficult. In addition, the DF and WO trees were quite complacent due to the fact they were growing in non-stressed conditions (as shown for WO in this area by Gildehaus et al. 2015) or that local factors (e.g. competition for resources with neighboring trees; Gould et al. 2011) had a greater influence on growth than climate. Furthermore, the DF trees were very young (~30 years old), thus undergoing rapid radial growth that likely varied among trees, thus confounding the relationship between radial growth and climate. These issues may explain the low EPS and interseries correlation values for some of the chronologies for these sites. Nevertheless, all the chronologies showed significant correlation to climate variables (on monthly or annual timescales) indicating that there was a common growth response to climate among the trees sampled.

Analysis of the tree-ring data was more complex for the JU site for two reasons: a) the *stressed* trees cored were different to the *stressed* trees used for the water potential measurements and b) the *stressed* trees apparently stopped annual ring production between 1956-2007. It is not clear whether the *stressed* trees stopped annual stem growth because they were severely carbon limited due to drought-stress. In only two cases, the last years of ring production corresponded to a severe, multi-annual drought period (around 1994 and 2002). In the other three cases, there were no severe droughts around the time ring production stopped and climate was average or wetter than normal. It may be the case that ring formation occurred asymmetrically around the stem (Ward 1982), although given that two perpendicular cores were taken from each tree it is unlikely that they would completely miss asymmetric rings. Some studies have reported continuously missing rings near the base or in the lower part of the tree stem when trees grow at the

edge of their distributional limit and are extremely stressed (Novak et al. 2011; Wilmking et al. 2012). This is because ring formation begins near the branches where the products of photosynthesis are readily available and there are the highest amounts of growth-inducing hormones and may not reach all the way down the stem. Thus perhaps ring formation had stopped occurring at breast height in the *stressed* juniper trees, though it is still surprising that this was occurring for so many decades.

7.9 General methodological issues

To aid the interpretation of the Ψ and tree ring data, it would have been useful to have collected a variety of extra data. In particular, starting Ψ measurements a few months earlier and/or continuing monthly measurements during the autumn would have provided pre- or post-drought baseline values with which to compare peak-drought values. Post-drought conditions would have been particularly interesting to understand whether there was a significant difference in the rate and extent of recovery of Ψ in *stressed* compared to *healthy* trees. Knowing when canopy loss began at each of the sites would also have helped elucidate the relationship between drought stress and canopy loss. It is unclear whether canopy loss began before peak summer drought conditions or whether it was a response to summer drought conditions and tree drought stress. Other desirable data include soil moisture data, stomatal conductance, photosynthesis and transpiration which would definitively show the degree of drought-stress experienced by the trees.

Furthermore, to draw more robust conclusions about interspecific sensitivity to drought, it would have been necessary to have several study sites for each species. Replication would have enabled species averages to be constructed, which is particularly important since drought sensitivity can vary within a species depending on site-specific climatic conditions and stand characteristics such as age and density (Bréda et al. 2006; Meinzer et al. 2010; van der Molen et al. 2011; Berner and Law 2015). This would also have allowed a greater sample size for *healthy* and *stressed* trees which would in turn have enabled more robust statistical analyses. However, due to time and financial constraints, it was not possible to collect such data.

Finally, the 10% canopy loss threshold chosen to define *stressed* versus *healthy* trees was arbitrary. Differences between *healthy* and *stressed* may have been more obvious if trees with a larger proportion of canopy loss had been selected, particularly as studies have shown that even 50% canopy loss may have no significant effects on tree growth (Miller 1990; Pataki et al. 1998). However, it was sometimes difficult to find and/or access trees with such high canopy loss. Trees were usually selected because they were close to each other, had a convenient *healthy/stressed* neighbor and had easily accessible canopies. Furthermore, it was sometimes difficult to estimate how much canopy had been lost and to differentiate canopy loss due to drought rather than ageing or shading of branches.

7.10 Future research directions

There are still many gaps in our understanding of how foliage loss relates to the physiological response of trees to drought stress. The literature review for this thesis revealed very few studies linking physiological measurements to drought-related canopy loss. More long-term measurements of canopy cover such as the European International Cooperative Program on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests 2011) coupled to physiological measurements such as water potential, transpiration and stomatal conductance are needed to explore the mechanisms behind defoliation and how they are related to climate.

The species examined in this thesis clearly showed different patterns of Ψ during drought, depending on their hydraulic strategy (isohydric versus anisohydric) and factors affecting individual trees (e.g. rooting depth, competition for resources, micrometeorology). More research is needed on the main factors affecting Ψ and whether plants exhibit any threshold-type responses that lead from drought stress to mortality. Better knowledge of these factors may help understand why some of the DF trees recovered their Ψ in September but others did not. Furthermore, more thorough experiments to elucidate whether species are isohydric, anisohydric or somewhere in between may help clarify the expected response of their Ψ measurements to drought and help model these processes.

8. CONCLUSIONS

The weather during the summer of 2015 and in the year prior was warm and dry compared to baseline conditions, probably due to warm sea surface temperature anomalies in the northern Pacific Ocean. These drought conditions led to substantial reductions in midday Ψ_{leaf} and Ψ_{pd} in all four species measured compared to “pre-drought” literature values. As a result, all the species experienced significant losses of hydraulic conductivity and extended periods of stomatal closure. However, Ψ_{min} values reached by the species were not exceptional compared to literature values, except at the DF site. The DF trees experienced the most severe drought stress, in some cases leaving them unable to recover as drought conditions eased at the end of the summer.

There was no clear relationship between foliage loss and the level of drought stress experienced by the trees for any of the species except Douglas-fir which showed significant differences in Ψ between *stressed* and *healthy* individuals. Analysing this relationship was difficult without measurements of stomatal conductance, transpiration or longer-term measurements of Ψ . Furthermore it can only be speculated whether foliage loss was a direct consequence of tree drought stress during the summer 2015 or had begun prior to the onset of drought. Species hydraulic strategies (isohydric versus anisohydric) and differences in rooting, soil water availability and water use of individual trees appear to play an important role in determining the Ψ of *healthy* and *stressed* trees.

Finally, for the three species where tree-ring analyses were performed, there were some prior differences in growth rate, variability and climatic sensitivity between *healthy* and *stressed* trees but these differed between sites. Larger sample sizes and site replicates would improve the robustness of these conclusions and more research is needed to fully explore the physiological and structural processes mediating tree drought stress. Nevertheless, this study provides a unique insight into the physiological response of four tree species to an exceptional drought event in a region where continued warming over the coming century will likely exacerbate the frequency and severity of drought events.

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