

AN ABSTRACT OF THE THESIS OF

Randi C. Shaw for the degree of Master of Science in Forest Ecosystems and Society presented on July 28, 2016.

Title: TREE VIGOR RESPONSE AND COMPETITIVE ZONE DENSITY IN MATURE PONDEROSA PINE.

Abstract approved:

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This study explored the relationship of mature ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) tree vigor and competitive zone density following thinning and fuel reduction treatments. Competitive zone density (CZD) was defined as the total tree basal area (m²/ha) surrounding a given ponderosa pine tree within a 10m fixed radius plot. The vigor of 60 trees were observed at two separate mature ponderosa pine stands in south-central Oregon, Lookout Mountain (LM), and Sycan Marsh (SY). Tree vigor response was measured using three physiological metrics: xylem sap flow (kg/day), bole water potential (MPa), and resin exudation (ml/day). Dominant and co-dominant pines were chosen across the available range of CZD at each site. Data were collected over the course of one growing season in 2015, from late June to early October.

Sap flow was recorded at four 6-day periods over the season to incorporate the influence of seasonal moisture decline on tree physiological response. Water potential was observed twice, at mid- and late-season. Resin exudation was observed in August to correspond generally with flight periods of various bark beetle species. To account for environmental influences on tree physiology, soil volumetric water content (SWC, m³/m³) was measured approximately every 3-4 weeks and daily potential evapotranspiration (PET) data were obtained from the Western Regional Climate Center's Remote Access Weather Stations (WRCC RAWS) archives. Data were analyzed using a linear mixed model including both environmental and competitive variables.

A quadratic relationship between post-thinning CZD and sap flow was evident, indicating a positive but highly variable association up to a threshold of roughly 40 m²/ha. Above this density threshold sap flow

declined markedly, suggesting that tree competition becomes an important factor in constraining water resource access in these sites at higher densities. Bole water potential in mature ponderosa pine was also related to CZD at the LM site. Resin exudation showed disparate relationships to CZD by site and may be more directly influenced by factors other than CZD. Overall tree vigor was higher at LM despite comparatively lower SWC, potentially due to the greater size or age of the study trees. The positive correlation of vigor and CZD up to the middle density range implies that there may be facilitative effects of adjacent trees to be considered for mature ponderosa pine, especially when reducing drought vulnerability is a management goal.

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TREE VIGOR RESPONSE AND COMPETITIVE ZONE DENSITY IN
MATURE PONDEROSA PINE

by

Randi C. Shaw

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented July 28 2016
Commencement June 2017

Master of Science thesis of Randi C. Shaw presented on July 28, 2016

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Randi C. Shaw, Author

ACKNOWLEDGEMENTS

A phrase that has influenced all aspects of my graduate school experience, from application to culmination, has been: the more you know, the more you owe. There is absolutely no doubt that I have learned more than I could have imagined possible, and that I owe so many to be able to have reached this point. The debt to pay forward as I move into life's next adventure is delightfully enormous.

So many thanks...to my first co-advisor, Dr. Paul Doescher, who is the reason that I found a place in the College of Forestry and who continued to supply me with his enthusiasm after his retirement and despite his own considerable challenges. To Dr. Paul Anderson, my principal advisor, for sticking with me these two years on this project, and for being my foremost example of intellectual integrity. To my co-advisor Dr. Dave Shaw for allowing me to come out of nowhere and turn him into my sounding board, my source of school-life advice, and for being a relentlessly cheerful advocate. To Dr. Jane Smith, for her open door, her warm-hearted lab group, her supportive voice, and her female perspective. To Dr. Chris Still, for allowing me to co-opt him into my committee in year two and for engaging me with his lab group. Huge thanks to Ariel Muldoon and Dr. Lisa Ganio - without them I would be statistically insignificant. To Dan Mikowski, for calmly keeping me afloat in a stressful field season, with donuts and the Cleopatra stick at the ready. To Amy Barnhart, for being engaged and flexible and fun as my main field help, and Doni McKay, for data management support extraordinaire. To Dr. Sara Robinson for serving as my GCR with such gusto. To Dr. Troy Hall for being a mentor and inspiration in my degree pursuit, career and beyond. To Dr. Randy Rosenberger for his belief in me and unconditional support of the choices I made. To Dr. Nancy Grulke, for sharing her study sites, considerable equipment and even more considerable knowledge. To Craig Bienz, Mark Hedrick and all the Sycan Marsh Nature Conservancy folks who gave me information, equipment and their personal support. To Dr. Rick Meinzer for psychrometry support and crucial water potential advice, Dr. Matt Powers for silviculture knowledge, Kelly Christianson for GIS problem-solving, and a multitude more without whom I would not have had a whisper of a chance of realizing this project. And of course to the US Forest Service PNW Research Station for my graduate assistantship and generous support in so many avenues, and to the OSU College of Forestry for the invaluable education and personal consideration I have received from the day I walked onto campus.

Then there are those that made the rest of my graduate school experience the mind- and heart-full one that it has been. This is not the right place to name them all, but for those that believe in the importance of bringing all kinds of voices into environmental work, who have worked hard in the College to promote more perspectives and who use what they know to pay what they owe, I am incredulous and grateful. Gracias a

todos en Valdivia y aquí en Corvallis para una experiencia increíble en Chile; para su apoyo, su paciencia y su amistad. I know myself well enough to know I would not have survived a day without my social support-network of friends, colleagues, coaches, family and beyond. I now stand in awe of my mother and father for getting their graduate degrees with two small children and full-time jobs, and even more so of my grandmother for achieving her PhD through the distinct challenges faced as a black woman in America - and then paying it forward her whole life through supporting her community.

I will strive to do the same.

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CHAPTER I – INTRODUCTION, CONCEPTUAL FRAMEWORK, AND RESEARCH QUESTIONS

Introduction

The study of mature ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) tree vigor after restoration treatment is highly relevant considering the emphasis on preserving large, old trees in Oregon's landscape. This emphasis comes in part from habitat protection requirements as a result of species protection law (ESA 1973, USDA and USDI 1994, Tuchmann et al. 1996), which has led to harvest restrictions of trees greater than 21 in diameter on federal lands east of the Cascade crest. It also stems from a desire to increase resilience in Pacific Northwest forests in the face of a likely hotter and drier climate of the not-so-distant future (IPCC 2013). The presence of mature trees in a forest contributes to many aspects of forest persistence, such as genetic, age and structural diversity, resistance to fire, increased water availability, biodiversity, and contribution to carbon storage (Franklin et al. 2013). In the dry forests of eastern Oregon, ponderosa pine is a key ecosystem component. Management, therefore, often centers on leaving mature pines in place while reducing the surrounding plant competition (Kolb et al. 2007).

Retaining mature ponderosa pines, or any species, is only worthwhile if the retained trees have sufficient capacity to persist. In general, studies of older (>100 years) ponderosa pine stands are less prevalent, due to a research focus on plantation silviculture combined the loss of old-growth specimens to past timber harvest (Sesnie and Bailey 2003). Therefore many unknowns remain concerning specific management for older and larger ponderosa pines. Is merely retaining large ponderosa pines in eastside Oregon forests sufficient for their perpetuation in the landscape? Or are there finer-scale considerations to be made regarding restoration prescriptions for mature trees?

Conceptual Framework

A tree's capacity to use resources and to allocate energy to growth and protective behaviors are indicators of tree vigor. Tree vigor, the ability of a tree to grow in its environment based on available resources and disturbance influences, is seen as a way to gauge resiliency, a major goal of ponderosa pine forest management (Franklin et al. 2013). Vigorous trees are thought to better resist or recover from disturbances such as drought, fire, pests and pathogens (Larsson et al. 1983). As growing space plays a major role in the proportion of resources available to a given tree, surrounding tree density is an important determinant of competitive pressure and therefore vigor.

When competition is reduced through thinning or burning, the limiting resources are potentially made more readily available for distribution among (fewer) remaining trees. Therefore it can be surmised that reductions in competition increases available resources, leading to increased vigor of retained trees, assumptions supported by other investigations of ponderosa pine physiological response to thinning (Feeney et al. 1998, Zausen et al. 2005). This triangle of interaction formed the underlying conceptual framework of this study (Figure 1).

While it is known that treatments such as thinning and burning can benefit forests in terms of growth and productivity while lessening severity of post-treatment disturbance (Oliver 1990, Wallin et al. 2004, Kolb et al. 2007, Fulé et al. 2012, Hessburg et al. 2016); the effects of these treatments on water use and self-defense are less understood. Understanding these responses is important, however, as a tree's use of water, nutrients and other site resources and employment of self-defense mechanisms are critical elements of tree survival. Given the likelihood of decreased water resources in coming decades due to global climate change, with substantial effects on tree mortality already being seen in many areas of the United States (Millar and Stephenson 2015), such investigations are more important than ever.

Research Questions

To address the important considerations of resource availability and management in the context of old-growth ponderosa pine, this study looked at the physiological relationship of mature tree vigor and competition, seeking to characterize the relationship of competitive density at the individual tree scale. The principal question was: **how does tree vigor in mature ponderosa pines of south-central Oregon vary with competition after thinning and burning?**

More specifically, this investigation focused on two questions:

How does mature tree vigor vary with surrounding tree density at the individual scale (within a 10m radius)?

What density among mature trees is needed to sustain the vigor of retained mature trees?

Three physiological metrics were used to assess vigor: xylem sap flow (water use), bole water potential (water status), and oleoresin exudation (self-defense). Because available moisture is an important influence on water use, and moisture generally declines in dry forest systems over the course of a seasonal drought, looking at sap flow and water potential over time was an inherent part of answering these questions. These indices of

water use, water status, and self-defense capability provide meaningful indications of ponderosa pine vigor, and furthermore are likely to be affected by near-term changes in forest density after thinning and burning. The interest in *individual* scale competition, as opposed to stand or broader scale density, stemmed from the fact that resources are accessed – and competed for – at this scale. The extent of a tree’s canopy and roots constitute the majority of its contact with water, light and nutrients. No exact measurement can define this, but for ponderosa pine in the 100-150 year age class, twice the width of an average tree canopy (which in these sites was ~10 m) was considered a useful estimate, as this was thought to encompass the bulk of its root system, though not its full extent (see Chapter 2).

The following *a priori* hypotheses about the nature of mature pine vigor and individual-scale density were explored: 1) sap flow and water potential were expected to decline with soil moisture decline over the course of the season; 2) all measures of tree vigor were expected to decrease linearly with increased competition; and 3) given similar environmental conditions at the two study sites – or in spite of some differences – similar trends in response were expected for the trees at each site.

Goals

The overarching goal of this investigation was to enhance dry forest management strategy in light of changing stand dynamics, management priorities and climatic conditions. The ever-growing concern of how to best manage for climate change and its likely consequences is highly significant and presents novel challenges for managing ponderosa pine and other dry forests (Kolb et al. 2007, Millar et al. 2007). As young stands mature, managers will need information on how these older age classes may best be supported toward resiliency and productivity goals. It is important to actively consider larger, older trees beyond the broad brushstroke of retention if they are to be effectively maintained in the landscape. Adding to our understanding of mature ponderosa pine physiology will help inform these management challenges. In better defining tree vigor response within a range of residual densities, we can open the door to possible alternatives for enhancing ponderosa pine stand resilience.

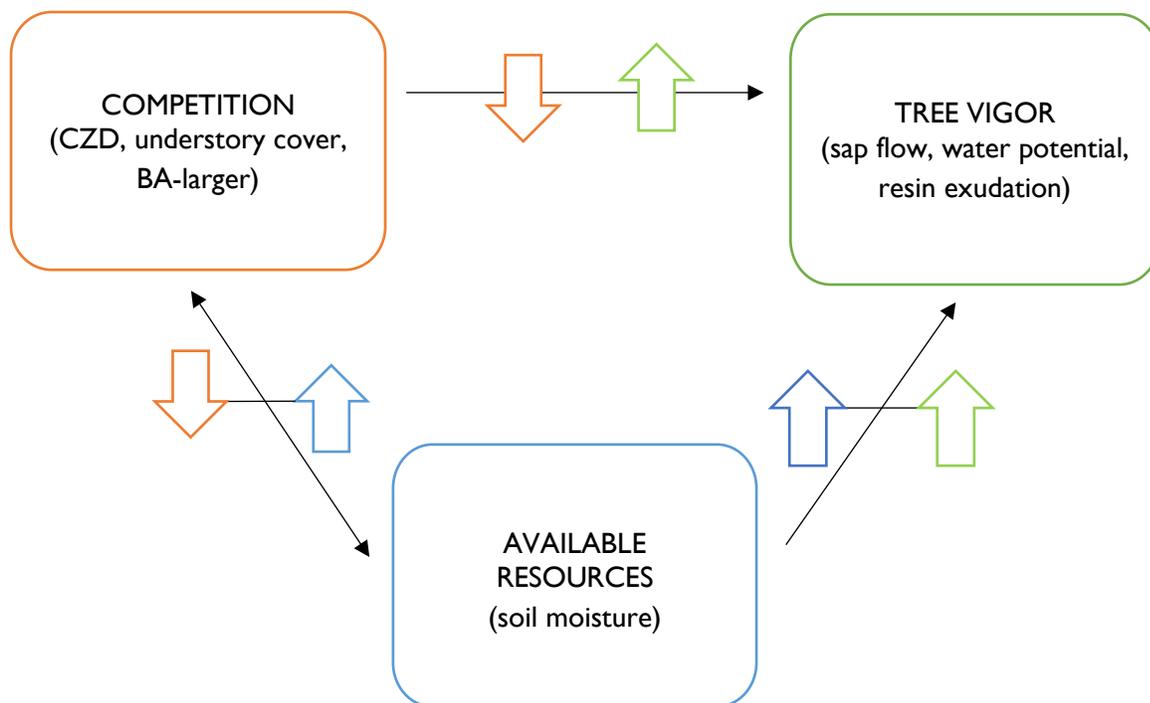


Figure 1. Illustration of original conceptual framework for relationships between competition, vigor and available resources for trees. As competition is reduced through management actions such as thinning or burning, more resources are available for fewer trees (orange – blue arrows). Increased resources supports greater tree vigor (blue – green arrows). Therefore, as competition is reduced, tree vigor is hypothesized to increase (orange – green arrows). The metrics used in this study to address each aspect of the 3-part relationship listed in parentheses.

CHAPTER 2 – A REVIEW OF PONDEROSA PINE AND ITS MANAGEMENT

Ponderosa pine

Description

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) is a widely distributed conifer species in low-to-middle elevation dry forests of the American west. The species occurs in areas where annual precipitation is as low as 205 mm per year and the majority of precipitation falls in the winter months, leading to annual summer drought (Oliver and Ryker 1990). In these areas the annual temperatures generally fall between 5° and 10° C, with average temperatures in July-August from 17° to 21° C. Ponderosa pine's tolerance for low-moisture conditions contributes to its extensive geographic range, stretching from lower Canada south to Mexico, and from Nebraska and Oklahoma to western Washington, Oregon and California. As a result of a drier climate, these forest-types are characterized by frequent, low-intensity wildfires. However, ponderosa pine is considered to be fire-resistant upon reaching sapling size, with thick bark and a 50% or greater chance of surviving a fire event if less than half the bole and crown are scorched (Oliver and Ryker 1990, Thies et al. 2008).

Sapwood thickness in ponderosa pines is large compared to many other conifer species, which allows for a greater volume of water transport and storage. Though this has caused ponderosa pine to be fairly vulnerable to embolism - the formation of air bubbles that block water movement in the xylem – it is thought that the overall increase in capacitance of sap flow due to thicker sapwood and greater ability to move water laterally in the stem (radial conductivity) generally offsets this vulnerability (Martinez-Vilalta et al. 2004). Ponderosa pine, as compared to other tree species, also tends toward lower sapwood:leaf area ratios, which reduces the transpiration demand from the canopy on the rest of the tree architecture. Ponderosa pine's isohydric strategy of stomatal closure in very dry conditions, which is triggered at leaf water potentials around -1.7 MPa (Meinzer et al. 2004) and progresses to complete canopy closure at water potentials of between -2 and -3 MPa (Martinez-Vilalta et al. 2004), also offsets embolism vulnerability (Richardson 1998), though it potentially can lead to mortality under prolonged drought conditions (Martinez-Vilalta et al. 2004). Ponderosa pine also performs well in moisture-scarce areas due to an ability to grow prodigious tap-roots over 2 m deep in porous soils and up to 24 m deep in some conditions (Stone and Kalisz 1991), as well as lateral roots that can extend over 46m in open stands (Oliver and Ryker 1990). Stone and Kalisz (1991), in their compilation of studies on rooting extent in several tree species, reported observed root radii from 6.1 – 25.6 m for ponderosa pine.

Importance of larger trees

Ponderosa pine grows to sizes upwards of 260 cm diameter at breast height (dbh) and 70 m high, and is known to live for hundreds of years (Oliver and Ryker 1990), making it a critical component in dry forest functions and interactions. As it matures, ponderosa pine retains strong physiological capabilities, with trees up to 200 years observed to respond to reductions in competition (Boldt and Van Deusen 1974). Mature pines in a stand can therefore potentially benefit from thinning and burning treatments and contribute significantly to processes such as ecosystem water balance. For example, Ryan et al. (2000) found that both whole-tree conductance and transpiration were lower for older, taller trees than younger trees (290 years and 36 m compared to 40 years and 12 m) in the same conditions. The authors speculated that a significant presence of mature trees in the landscape, by using comparatively less water, could enhance ground and surface water flow, thereby enabling faster decomposition rates and greater nutrient availability for the system. In ponderosa pine forests, there are few other plant species that grow large enough to offer this benefit.

As ponderosa pine matures and develops a more complex root system, it expands its ability to source water. It has been documented that ponderosa pine is quite effective at extracting water from bedrock and high porosity soils, a part of its drought avoidance strategy in dry climates (Stone and Kalisz 1991). This water is in part redistributed to upper soil layers through the mechanism of hydraulic redistribution, a passive process caused by changes in root pressure as a result of daily transpirational flux. Both the shallow roots of the pine itself as well as other vegetation are able to capitalize on an increased soil moisture balance as a result (Caldwell and Richards 1989).

Management of ponderosa pine systems

Concerns

Many fire-adapted forests, including ponderosa pine, have become progressively vulnerable to high-severity wildfires and subsequent pest/pathogen infestation due to increased fuel densities. This is largely as a result of fire suppression policy and other human impacts on the forested landscape, such as grazing and timber extraction (Kolb et al. 2007). The outcome of anthropogenic influence has largely been a higher density of smaller trees, understory plants, and woody debris than was historically present in most dry forests (Agee 1993). Climate change adds to disturbance vulnerability; as global temperatures continue to rise in the next decades, it is likely to increase drought frequency, intensity, and duration (CIG 2004). This scenario will increase competition among vegetation for dwindling resources (Franklin et al. 2013). Higher competition

decreases tree performance, increases stress, and therefore contributes to the likelihood of major pest or pathogen outbreak or catastrophic fire – ultimately leading to tree mortality and ecosystem alteration (Kolb et al. 2007, Lloret et al. 2011, Asner et al. 2015).

Increasing levels of tree mortality across a range of forest types have been occurring across North America (Allen et al. 2010, Anderegg et al. 2012, Millar and Stephenson 2015). Much of this increase is attributed to the effects of persistent, frequent drought and pest and pathogen epidemics. Wildfire activity, often exacerbated by drought, has also been on the rise, with a record-setting 10.1 million acres burned in the US in 2015 (NIFC 2016). (The previous record was set only nine years prior in 2006.) Over two million acres of this wildfire activity occurred in Washington and Oregon alone. The risks of wild fires and forest loss to ecosystems, economy and public health and safety have spurred action in the scientific and land management communities (Spies et al. 2006, Franklin et al. 2013).

Stand management techniques

In the interest of addressing the issues of fire suppression and disturbance severity through management, how ponderosa pines respond to thinning, prescribed burning or other restoration treatments has been an active area of scientific research (Covington et al. 1997, Wienk et al. 2004, Simonin et al. 2007, Keane et al. 2009, Day and Pérez 2013), and management policy and strategy (Franklin and Agee 2003, Emmingham et al. 2005, Apostol and Sinclair 2006, Franklin et al. 2013). Thinning of suppressed or intermediate trees (at times referred to as thinning from below) is generally employed in silviculture to focus growth on fewer, dominant trees. Increased growth by the residual trees is possible because of the increased space and resources created as a result of removing a portion of the stand basal area (Tappeiner et al. 2015). Conversely, there is a stand density at which some portion of trees begin to be suppressed and the probability of mortality due to competition is increased. Many calculations for estimating growth and productivity as well as determining density thresholds exist to guide stand management. For stands with reduced growth yield capacity, such as is true for some areas where ponderosa pine occurs, a calculation referred to as the upper management zone (UMZ) was developed. It is based on the species, plant association, and stand density index of the stand, and usually represents 75% of the stand density index of a “normally” stocked stand. Bringing a stand’s total basal area below its UMZ threshold can alleviate density-dependent mortality and aid in meeting other management objectives such as increased resistance to disturbance (Cochran and PNW Research Station 1994).

Fuels reductions in overstocked stands can lead to an immediate growth response regardless of age or origin, while conversely mortality appears to increase noticeably with stand density (Biondi 1996, Sesnie and

Bailey 2003, Oliver 2005, McDowell et al. 2006). One study of ponderosa pine in Montana found decreases in several metrics of tree growth and vigor with increasing competition over a range of tree sizes (Woodall et al. 2003). Study of old-growth forests in western Oregon, including ponderosa pine, have shown that thinning consistently increased basal area growth by at least 10%, and that these effects on growth rate persisted for 20 years or more (Latham and Tappeiner 2002). McDowell et al (2003) similarly found evidence that stomatal conductance, net photosynthetic rate and basal area increment increased after thinning of 250 year-old ponderosa pine stand in Oregon, and were increased relative to un-thinned stands for at least 15 years. Use of thinning and prescribed burning among other treatments has been shown to reduce wildfire severity in ponderosa pine forests (Pollet and Omi 2002). Thinning has been connected to decreased bark beetle incidence in ponderosa pine stands due to removing susceptible trees and increasing residual tree vigor (Larsson et al. 1983, Eckberg et al. 1994, Negron et al. 2000, Fettig et al. 2007, Fettig et al. 2012), but as only some beetle species focus on suppressed trees, the use of thinning from below in mature stands may not reduce beetle-induced mortality (Cochran and PNW Research Station 1994). Prescribed fire may attract beetles and undermine the benefits of reduced fire risk for older trees according to some research (Perrakis and Agee 2006) or not, according to others (Zausen et al. 2005, Hood et al. 2015). Studies on the effects of prescribed burning on older ponderosa pine are not as prevalent (Kolb et al. 2007). Instead, fire effects research in older ponderosa pines has often focused on post-fire mortality (Fulé et al. 2002, Agee 2003, McHugh and Kolb 2003, Woolly et al. 2012). Older ponderosa pine in overstocked stands may be more vulnerable to post-fire mortality due to existing wounds that allow fire to penetrate deeper and higher (Linder et al. 1998), because of copious leaf and bark litter production that increases fire intensity nearer to the tree (Sackett and Haase 1998), and because their thicker phloem is attractive to the parasitic beetles that regularly infest stands after a burn event (Breece 2006, Perrakis and Agee 2006).

Desired outcomes

Structure, composition, density, and spatial arrangement of the forest as a result of management action are more frequently studied outside the narrow context of economic yield. Much of the scientific and management literature recommends replicating historical forest conditions and their range of variability (Covington et al. 1997, Moore et al. 1999, Franklin et al. 2013), though opinion on this is shifting as uncertainties about future climate are considered (Millar et al. 2007, Chmura et al. 2011, Keenan 2015, Millar and Stephenson 2015). Prior to Euro-American settlement of the western United States, ponderosa pine forests of eastern Oregon were described as low-density (~13 – 59 trees per acre), dominated by large-diameter trees (>53 cm diameter), and characterized by frequent, low-intensity fire regimes (Franklin et al.

2013). In current management thinking, thinning for a low-density “clumped” or “patchy” tree distribution in ponderosa pine is believed to create a landscape that represents historical conditions, and facilitates beneficial ecological processes (Youngblood et al. 2004, Larson and Churchill 2012). This spatial arrangement includes clumps of trees, individual trees, and gaps where no trees are present. The forest ecosystem is considered to be more resilient (able to recover from disruption) because there are opportunities for a range of disturbances, modes of regeneration, and growth habits (Stephens et al. 2009). A clumpy-patchy arrangement creates different levels of competition at the individual tree scale, with some trees experiencing little to no competition in the immediate vicinity while others vie with several trees and plants for shared resources. The range of competition that would also support mature trees within a context of varying density is yet to be clearly identified, however.

Advancement in our understanding of how our ecosystems function and the impacts of humans on them have shifted management strategies to look at a wider range of needs and benefits (Allen et al. 2002, Kolb et al. 2007, Franklin et al. 2013). One notable response to this shift was the advent of the Eastside Screens, part of a series of standards and guidelines under what is collectively called the Northwest Forest Plan (USDA and USDI 1994, Tuchmann et al. 1996, Davis et al. 2011), a set of plan amendments incorporated into federal lands management in Oregon, Washington and Northern California in 1994. In the interest of universally preserving larger trees in forests east of the Cascade Range, east-side screens set harvest size limits at a maximum of 21 in dbh (USDA and USDI 1994). Motivated by mandated protections for northern spotted owl and other endangered species (ESA 1973), this policy is a key example of the dramatic changes in priorities, thinking, action (and revenue) for forest management on public lands in the western United States (Davis et al. 2011). Both science and management more frequently advocate for retention of mature trees as part of restoring late-successional conditions in the forested landscape (Kolb et al. 2007, Franklin et al. 2013). Part of the drive to increase late-successional forest is to increase the availability of habitats for a range of old-forest associated species, such as spotted owl. While these owls and other animals require larger, older trees for habitat, other wildlife use late-successional and old-growth forests in different ways. Thinning and burning has been shown to increase understory plant diversity and richness in ponderosa pine forests (Dodson and Peterson 2010), which in turn supports a range of other organisms (Mannan and Meslow 1984, Converse et al. 2006).

CHAPTER 3 - MEASURING TREE VIGOR BY PHYSIOLOGICAL MEANS

Tree vigor has often been calculated as a function of canopy growth and wood production (Waring 1980), and many studies have used this index to describe the productivity of a tree in relation to considerations such as beetle susceptibility (Larsson et al. 1983, Coops et al. 2009, Scherer et al. 2016). Other morphological characteristics such as live crown ratio or height to diameter ratio have been assessed as well (Emmingham et al. 2005) and crown dieback (Arthur et al. 2015). However, tree vigor can also be thought of in terms of the ability to access needed resources and withstand disturbance. This interpretation of vigor is more appropriate when managing for ecological goals rather than harvest targets, and when factors such as drought resilience, habitat value and disturbance resistance are more important than wood volume. The vigor of a tree can be observed physiologically in a number of ways. For dry forest systems, where water is a principal limiting resource, measures related to water use are especially relevant. Tree water use has been examined across a wide range of scales, from the leaf, root, or whole tree level, up to the ecosystem, landscape or global level (Zausen et al 2005, McDowell et al. 2006, Simonin et al. 2006, Kolb et al. 2007, Simonin et al. 2007). The number of approaches vary even more widely, ranging from stable isotope analysis, pressure chamber measurements for predawn/midday water potentials and other assessments, use of high-pressure flow meters to measure root conductance, and many others (Meinzer et al. 2001). Effective defense against environmental threats is another key aspect of tree performance, and has most frequently been studied in ponderosa pine through resin production (Christiansen et al. 1987, Phillips and Croteau 1999, Davis et al. 2011, Hood et al. 2016).

For this study, sap flow and water potential were selected as indicators of tree vigor because of the central role that water plays in ponderosa pine ecosystems, and because of the serious concerns over drought intensification in these forests. Additionally, the ability of a tree to utilize adaptations against damage and infestation are important to understanding its ability to persist through disturbance. Resin exudation, a key self-defense mechanism in ponderosa pine, was also observed for this reason.

Sap flow (tree water use)

Sap flow, which is the passage of water, nutrients and hormones through a plant, is an important metric for ponderosa pine physiological research (Oliver and Ryker 1990). Movement of sap through a tree's vascular system relates directly to all processes necessary for maintenance, growth, and reproduction, as it

carries water and nutrients upwards and photosynthetic products down. In order for a plant to live and grow, it must have the energy provided by the carbohydrate output of photosynthesis and the array of nutrients it absorbs from the environment, as well as the water that carries these (Taiz et al. 2015). Nearly all aspects of water use, as well as all physiological processes, have a link to the flow of water and its solutes through a tree.

Sap flow is initiated at the root zone. Trees and plants absorb water in the soil based on pressure potential differences between the inter-particle spaces in soil and the tips of roots, root hairs and their mycorrhizal colonizers. These pressure differences increase up the length of the tree, becoming extremely negative at the crown level. The generally-accepted cohesion-tension theory states that these large pressure gradients pull water up through the xylem and eventually out the open leaf stomata, a process known as transpiration. Cohesion and adhesion are the molecular forces that allow water to move in a continuous column through the tree rather than in separate molecules. These forces occur as a result of hydrogen bonding, which causes water molecules to 'stick' to each other as well as to the xylem surface as they are pulled upward. The loss of water at the leaf level is a consequence of necessary gas exchange through the stomata for photosynthesis and respiration (Taiz et al. 2015).

Driving water loss at the crown and influencing the water available at the roots are a number of environmental factors, including: vapor pressure deficit, solar radiation, wind speed, temperature, precipitation and soil moisture (Jones 1992). These drivers are in turn mediated by physiological adaptations, rooting depth, stem volume and leaf area of a particular tree (Sperry et al. 1998, Martinez-Vilalta et al. 2004). It is further affected by the overall presence of vegetation and competitive pressure on the water resource.

Sap flow measurement of the xylem is a measure of transpiration. The measurement is comprised of an estimate of vertical rate of ascent – sap velocity – and an estimate of the cross-sectional area of sapwood conducting sap. By incorporating the cross-sectional area of the trunk over which sap movement occurs, the velocity of sap can be converted to volume of sap moved per unit of time (Percy et al. 1991). Consequently, sap flow indicates both how much water the tree is taking up in its root system and how quickly that water is being moved up the stem. Higher rates of sap flow can be indicators of greater soil water availability and/or recharge of water stores, increased water loss (e.g. through stomata opened for evaporative cooling), or higher photosynthetic rate (because the stomata are open for increased CO₂ uptake). Therefore an understanding of available moisture, temperature, solar radiation, atmospheric humidity, and leaf area are also necessary for ascertaining the likely meaning of a particular rate of sap flow (Taiz et al. 2015). In this study sap flow was measured by use of heat dissipation probes, which allows for calculation of a velocity measurement from a

temperature difference value (see Methods), but it can also be observed through null-balance techniques and other approaches (Pearcy et al. 1991).

Water potential (tree water status)

While the mechanism of sap flow through the xylem and phloem brings water to cells, a moisture reserve in the vegetative tissue is necessary for this water to continue to move about, both through the system and in and out of individual cells. Water potential is a measure of the amount of potential energy provided by the water in a tree, and is reduced when the amount of water is reduced or its solute content increases. Dehydrated tissues with extremely low water potentials essentially have water ‘locked’ in place, as the few remaining water molecules lack sufficient energy to overcome the molecular forces of cohesion and adhesion (Taiz et al. 2015). Low water potential is a significant problem, as a prevailing need of all terrestrial plants is to maintain adequate turgor pressure throughout their tissues. Turgor is the cellular hydrostatic pressure that is essential for maintaining structural stability, regulating stomata, transporting elements across cell membranes, and several other important processes (Taiz et al. 2015). Maintaining turgor pressure requires a consistent presence of water and is a significant undertaking for a large plant such as a tree.

Water potential can be determined for tissues of foliage, stem, roots, or soil, each of which describe different parts of the hydrostatic pressure continuum and are influenced in different proportion by available moisture and environmental demand. Water potential is measured in units of pressure (e.g., MPa), subtracted from the ‘zero’ potential energy value of pure water. (For this reason water potential measurements of non-pure solutions are always negative.) As transpiration demand in plants existing in natural conditions shifts from near-zero at night to near-maximum at midday, the timing of water potential measurement must also be intentionally planned (Pearcy et al. 1991).

Tissue water potential can be observed using different methods including both pressure-chamber and psychrometric techniques. Psychrometry, which was used in this study, is based on calculating the vapor pressure of a sample of plant tissue (for this study, phloem bole tissue) in a sealed chamber. The vapor pressure of the sample tissue is first allowed to equilibrate with the air in the sealed chamber (assuming that the loss of water from the sample to the chamber during this time does not appreciably affect the water potential reading). Then the Peltier effect is used to condense water on the thermocouple junction of the psychrometer and the wet bulb depression of thermocouple temperature is recorded as the water evaporates from the junction – with the rate of evaporation being dependent on the equilibrated vapor pressure of the chamber and tissue sample. For this study thermocouple psychrometers were used with an applied cooling

current (Peltier effect) to achieve condensation. After the vapor pressure was recorded the cooling was stopped and the water allowed to re-evaporate. This caused a second period of cooling, but one that was mediated by the rate of evaporation, which was regulated by the vapor pressure of the chamber atmosphere and therefore the water potential of the sample (Pearcy et al. 1991, Brown & Bartos 1982).

Resin exudation (tree defense)

The first priorities for a tree for maintaining itself, according to the growth differentiation balance hypothesis (Herms & Mattson 1992), are root and leaf production, not self-defense. Still ahead of self-defense are height growth, diameter growth and reproduction (Smith 1997). These trade-offs are necessary for a plant to compete while at the same time survive in its environment. Once growth, maintenance and reproductive needs are met, a plant is better able to allocate energy to defense mechanisms. Given the resources a tree must expend to reach the point of effective self-defense, this makes a strong case for examining self-defense capabilities as an indicator of tree vigor.

A major disturbance in ponderosa pine ecosystems is beetle infestation, and one for which the species has developed specific protection responses, principally the release of oleoresins (generally referred to as “resin” in this study) to trap and eject the pests. Oleoresins are a complicated mixture of terpenoids and resin acids (Phillips and Croteau 1999), that when exuded serve several functions to protect the tree. First, they form a protective barrier over wounded tissue, which as the resin hardens seals the area off from further damage, infection or rot. In the case of pests such as bark beetles, the release of viscous and sticky resin can envelop the invading insects and force them out of the tree. This action is often referred to as “pitching out.” Therefore both resin pressure and volume are important factors for effective protection, and have been well-studied in ponderosa pine stands (Zausen et al. 2005, Wallin et al. 2008, Gaylord et al. 2011). Formation of resin ducts, from which resin is released, has been studied as a proxy for actual resin production, allowing for historical patterns to be detected (Lewisohn et al. 1991, Arbellay et al. 2014, Hood et al. 2015). Resin can be viewed from both constitutive and induced (as above) defense perspectives. From a constitutive standpoint, resin physical composition has been investigated through looking at viscosity and other physical properties (Davis et al. 2011). The chemical make-up of resin too has been studied, since this aspect of resin has complex relationships to pathogen resistance, beetle pheromones, herbivory, and other species interactions (Lieutier 1993, Phillips and Croteau 1999, Smith 2000).

CHAPTER 4 - STUDY SITES AND METHODS

Study Sites

Two sites were chosen within predominately ponderosa pine forests in south-central Oregon (Figure 2). Inclusion of two sites was considered useful in this study in order to avoid making inferences that could be due to the dynamics of one particular stand. Sites were selected in which thinning treatments for restoration purposes had taken place: the Lookout Mountain Unit at Pringle Falls Experimental Forest (USDA Forest Service) and Sycan Marsh Preserve (The Nature Conservancy). Within the sites 10 separate study areas were identified, herein referred to as neighborhoods.

Both sites are located along the eastern side of the Cascade mountain range in central Oregon, approximately 145 km apart north to south. Mt. Mazama deep pumice and ash deposits characterize the soil type (Simpson 2007). Ponderosa pines at these sites had stand ages over 100 years and were situated on southeast-facing slopes at ~1500m elevation. Both Lookout Mountain and Sycan Marsh experienced thinning and burning treatments within the past five years to reduce stand densities and thereby reduce risk to major disturbance. Portions of the stands representing pre-thinned conditions were present at each site, and were included in the study to represent the highest level of competing density.

In eastern Oregon, mean annual precipitation is 355-760 mm, falling mostly in winter as snow. Seasonal summer drought is common from July-September, with average rainfall less than 25mm (Oliver and Ryker 1990). Mean annual summer temperatures reach highs of 21 - 35°C (Adams et al. 2004). However, for the three years previous to the study severe drought conditions occurred over the summer months in south-central Oregon, with persistent moderate to severely dry intensities over July to September each year (U.S. Drought Monitor 2016). Higher-than-average dryness has characterized the region for a longer time period, with precipitation in the 25-50th percentile for 2011-2015. In 2015, this trend continued, with precipitation at 60-80% of average for the water year (October 2014 – September 2015), with a near-record low winter snowpack. Summer temperatures reached record or near-record highs across Oregon in 2015 (NOAA 2015).

The implications of recurrent drought conditions for this study were significant. First of all, to witness the effects of resource competition, it can be more effective to observe trees in situations where resources are scarce, so that advantages such as lower competitive density become more useful for the trees in question. Multi-year drought in the study locations certainly set the stage for water scarcity. Secondly, the repeated

occurrence, severity and early onset of the drought reflects earlier stages of the conditions that have historically influenced increasing tree mortality in California and other areas (Millar and Stephenson 2015, USFS 2016), and the effects on tree vigor can therefore be related more generally to widespread drought mortality concerns.

Lookout Mountain

The 1430 ha Lookout Mountain unit of Pringle Falls Experimental Forest (PFEF, lat. 43°42' N, long. 121°37' W) is located within the Deschutes National Forest, about 18 km west of La Pine, Oregon. Pringle Falls Experimental Forest is managed as part of the US Forest Service's national network of experimental forests and ranges set aside for conducting science and management research (Youngblood 2009). Before the advent of fire suppression practices, fire return intervals for this area were estimated at 7-20 years (Adams et al. 2004, Hagmann et al. 2013), usually occurring as low-intensity, low-severity events. However, prior to thinning and burning in 2011-2015, the site had experienced little fire disturbance since approximately 1845, in which a stand-replacing fire occurred. An additional fire occurred in 1914 over a section of Lookout Mountain, leading to current dominant stand ages of 170 and 101 years, respectively. In the 1970s, the site was low-thinned during the establishment of the existing road network. The lack of fire over the past century, as well as highly productive ponderosa pine growth at Lookout Mountain, resulted in these forests having more trees per hectare than expected under natural fire regimes in the late 20th century (Youngblood 2009).

Growing concerns in the early 2000s over Lookout Mountain's vulnerability to major disturbance, such as high severity fire, insect pest, or pathogen outbreak, presented an opportunity to study the effects of thinning and fuels reduction (Youngblood 2009). Beginning in 2011, an experimental restoration treatment plan was implemented at the Lookout Mountain site, using a complete randomized block design (Figure 3). Five levels of treatment were implemented in each of four designated blocks: no-action reference, thin from below to the upper management zone (UMZ, see Chapter 2), thin from below to 75% of UMZ, thin from below to 50% of UMZ, and thin from below to 75% of UMZ with regeneration cuts (gap areas) in 10% of the area. The experimental units were thinned and burned by block over the five-year period of 2011-2015.

For the purposes of this study Block 2 was used, as it was thinned in 2012 and underburned in 2014, fitting with the study intent of measuring recent post-treatment response. Tree ages ranged from 100 – 155 years. Block 2 has a predominantly south-facing aspect and an elevation range of 1530-1680m, with most slopes ~12%, though in one area of 27% (Neighborhood 04). Lookout Mountain's plant association in Block 2 is characterized as *Ceanothus velutinus-Arctostaphylos patula* (Volland 1985). This fits with on-site observations

of a principal understory component of *C. velutinus*, *A. patula*, *Carex stolonifera*, *Chrysolepis chrysophylla*, and *Arctostaphylos nevadensis*. Residual understory plant density was low across most areas of Block 2, though the understory cover for the study trees located in the un-thinned portion were notably denser (~60% compared to ~15% average density in thinned areas).

Sycan Marsh Preserve

Sycan Marsh Preserve (lat. 42°52' N, long. 121°06' W) constitutes 12,359 ha of private land surrounded by the Fremont-Winema National Forest, approximately 97 km southwest of Silver Lake, Oregon. It is owned and administered by the Nature Conservancy (TNC), a conservation organization seeking to protect the ecological resiliency and function of the forest and wetland ecosystems at the Preserve. Ponderosa pine and mixed-conifer forests are prevalent in the mid to upland areas of the preserve, transitioning to aspen (*Populus tremuloides*) groves intermixed with wetland and grassland systems as the slope flattens out toward the marsh zone (Bly Ranger District 2012). Similarly to Lookout Mountain, the historically frequent fire intervals of 7-15 years in this landscape were disrupted by fire suppression and other anthropogenic impacts including cattle grazing, causing changes in vegetation composition, structure, and density (Bly Ranger District 2012).

Within the greater forested area of Sycan Marsh, several areas have been targeted for forest restoration. This study focused on the Coyote Analysis Area where thin and burn treatments had been recently implemented, and at a nearby untreated area slated for first harvest in October 2015. Currently the management objectives established by TNC for Sycan Marsh are to establish a 400 year old forest with ~ 12 age classes. In the Coyote Analysis Area, thinning was carried out in 2006, leading to post-harvest densities of 2.27 m²/ha (196 trees (> 10 cm dbh)/ha), plus 62 saplings/ha (24%), and shifting the compositional dominance from a mixed conifer assemblage to ponderosa pine (94%). This was supplemented by prescribed burns in 2006 and again in 2013 in the forest and adjacent meadow (Bienz 2015).

An elevation of 1540 m was fairly uniform across the neighborhoods at Sycan Marsh. Slopes were negligible. Tree age was ~115 years for all sampled trees. Understory plant composition in the Coyote Analysis Area consists of rabbitbrush (*Ericameria nauseosa*), big sagebrush *Artemisia tridentata*), green manzanita (*Arctostaphylos patula*), as well as grass and herbaceous species including lupine (*Lupinus spp.*), strawberry (*Fragaria spp.*) and snowberry (*Symphoricarpus mollis*). Residual understory plant cover was proportionally high in grass and forbs with densities of 50 – 85% in all neighborhoods.

Neighborhood and tree selection

The sampling design was conceived to capture the gradients of competitive-level tree density present at each site. Vigor response was then observed over these density ranges. Competitive zone tree density (CZD) was measured in basal area (m^2/ha) in the zone of competitive influence, a 10m fixed-radius plot around each tree, or roughly twice the radius of an average (5 m as measured) sample tree canopy. While in this study 10 m was used to define the majority of individual tree root access, it is recognized that this was a rough estimate, and that 10m by no means encircled every root length. It is certainly possible that many of these mature pines surpassed this approximation for some of their roots, and were also competed with by trees whose roots were longer than 10 m.

An objective stratified sampling procedure was used to identify study trees over a similar range of competitive zone densities at each site. Density was first defined at the coarse site-level scale. Using 2014 orthophotos, all trees at each site were point-referenced in ArcMap 10.2.2 (ESRI 2013). Each site was subsequently delineated into one acre (0.4047 ha) polygons, each classified to one of five density ranges: 1-15, 16-30, 31-45, 46-60, or 61-upper limit (trees per acre/0.4047 ha). Using a random selection tool in ArcView, one GPS location per density level was randomly selected, resulting in 10 0.04-ha study areas, referred to here as “candidate locations.” From within each candidate location, “neighborhoods” of study trees were selected according to additional fine-scale criteria. Neighborhoods were comprised of six dominant or co-dominant study trees visually free of physical damage, defects or disease. Due to constraints imposed by sap flow measurement technology, all six trees had to be located within 30 m cable length from a centrally located data logger. Each neighborhood’s extent was therefore roughly a 30 m radius circle (Figure 4). In total there were 10 neighborhoods, five each at Lookout Mountain (LM) and Sycan Marsh (SY) (Figure 5). Overall, there were 60 study trees (30 per site) across the 10 neighborhoods. All neighborhoods were monumented at the center, and all study trees were GPS-referenced and marked with a numbered tree tag.

Data collection methods

Baseline data

For each study tree, baseline data were gathered on age, height, diameter at breast height (dbh, cm), sapwood radius (mm), live crown ratio (%), crown length (m), crown width (m), crown position (open, dominant, co-dominant, intermediate, suppressed), height to lowest limb (m), understory vegetation, and visible disease, damage or decay.

A 10 m fixed radius circular plot centered on each study tree was established to represent its zone of competitive influence. This distance roughly corresponded with a distance of 2 crown widths for trees in this size class, which corresponds with the general rooting extent of ponderosa pine (Curtis 1964). All trees over 5 cm dbh in each fixed plot were GPS-referenced and species, dbh, height, and crown position were recorded. Tree density in the zone of competitive influence was calculated in basal area (m^2/ha). From this, BA-larger (BAL), the proportion of total competitive zone basal area attributable to trees having a larger DBH than the study tree, was calculated for each study tree. BAL described the social status of the measured tree relative to its putative competing neighbors. To account for non-tree competition, an ocular estimate was made of the percent cover by each species of understory plant in each 10 m fixed radius plot (0.031 ha). For analysis, estimated cover of individual species was summed to a single percent cover value for the plot.

Neighborhood tree density was also described. A 10F or 20F prism was used at each study tree to estimate basal area in m^2/ha , and these results averaged for each neighborhood. At the neighborhood level, information was gathered on-site on elevation (m), slope (%), and aspect (cardinal direction). Elevation and aspect were recorded using a Trimble GPS unit. Slope was estimated using a clinometer.

Environmental influences

Daily potential evapotranspiration (PET) values were downloaded from the Western Regional Climate Data Remote Automatic Weather Stations (RAWS) archive (WRCC 2016). Two locations were identified, one in the vicinity of each study site. These locations were assumed to be reasonable representations of the climatic conditions of the study sites. PET values were calculated by the Western Regional Climate Center using the Penman equation (Penman 1948), and were not corrected for arid environment.

Volumetric soil water content (SWC) data were collected seven times over the 2015 season, including at each of the four sap flow sample periods. Soil moisture information was gathered using a Troxler Sentry 200-AP non-nuclear resonant frequency capacitance probe (Troxler Electronic Laboratories, Inc. Research Triangle Park, NC). To take moisture readings, two 5cm diameter PVC pipe soil moisture tubes were installed at each neighborhood, one under the canopy cover and the other at a canopy gap. The tubes were installed to a minimum depth of 50cm at all neighborhoods, and to a depth of 70-75 cm where soil conditions permitted. SWC readings were taken at 0, 15, 25, 40, and 50 cm, and 70-75 cm where possible. For sap flow and water potential analysis, a weighted average of all SWC values to 50cm depth per neighborhood was calculated for each sample period. For resin exudation analysis, a seasonal average of SWC by neighborhood was calculated.

Sap flow

Sap flow data were collected using the thermal heat dissipation probe (TDP) technique (Granier 1987). Vertically-arranged two-prong 50 mm probes were installed in the northeast side of the boles of all study trees at 1.5m. Each probe was sealed with putty and caulk, encased with foam insulation, and protected from solar radiation with a reflective shield to prevent fluctuations in sensor temperature and to avert moisture-related issues. The probes were connected to CR1000 or CR10X data loggers (Campbell Scientific, Logan UT) up a maximum cable distance of 30 m. The data loggers and probes in each neighborhood were powered by a 12-V battery backed up by a solar panel. Each probe heating element was continuously supplied a 5-V DC current. The temperature differential (dT) between the upper and lower probe elements was measured at 5 or 10 minute intervals, 24 hours per day. The measured temperature differential was converted to a sap velocity using equations developed by Granier (1987) below (1-2), and then to a volumetric sap flow rate, measured in cm^3/hr .

$$(1) K = (dT_M - dT) / dT$$

As shown in equation (1), Granier developed a dimensionless parameter for flow index (K), calculated from the maximum daily temperature differential (dT_M) occurring at zero flow velocity and the reading from the probe at a specific point in time (dT). Its empirical relationship to actual sap flow velocity was found to not differ significantly among a number of common tree species (Dynamax 1997), re-validated by Clearwater et al. (1999), and was therefore considered valid for computing sap flow in this study. Other studies (Simonin et al. 2006, Fischer et al. 2002) using the TDP approach for ponderosa pine similarly accepted this value for their calculations.

Velocity (v) in cm/s can be related to K by the following equation (Granier 1987):

$$(2) v = 0.0119 * K^{1.231}$$

Sap flow (Q_s) was computed by multiplying v by the cross-sectional area of the tree's active sapwood (A_s):

$$(3) Q_s = A_s * V * 3600 (\text{s}/\text{hr}) * 0.001 (\text{g}/\text{kg}) / 24 (\text{hr}/\text{day})$$

Q_s provided an estimation of whole tree water use and was reported in kg/day for this study. Cross-sectional sapwood area was gathered from tree core samples collected August 25th (Lookout Mountain) and September 1st (Sycan Marsh). Two cores per tree were collected, off-set by 90° to allow sapwood area to be

calculated as the area of an ellipse, avoiding uneven bole growth bias (Anderson 2011). Sap flow rather than sap velocity was chosen as the reported value for water use because flow provides a clearer picture of the amount of water moving through the system relative to the basal area present. Sap flow, as a volume measurement, also better corresponds conceptually with the volumetric soil water content data taken to characterize the moisture supply for each neighborhood.

The sap flow activity of each study tree was recorded continuously for a week at four sampling periods in 2015: early July, July/August, August/September, and September/October. In this study, there were only six data loggers available to record sap flow values for 10 total neighborhoods. Therefore, for each sampling period there were two weeks of observation. In week 1, neighborhoods LM/SY 01, 03, and 05 were recorded. In week 2, neighborhoods LM/SY 02, 04 and 05 were recorded. LM and SY 05 were chosen to run in every rotation as the effects of moisture-scarcity were assumed to be most detectable in the densest plots, where competition would be the highest (Table 1).

Water potential

Water potential was observed for each study tree at both sites at two points in the season, July 25-26th and September 24-25th, to observe changes over the season (Table 2). Water potential was measured on bole phloem tissue for all study trees using screen-caged thermocouple psychrometers with calibration chambers (83 series, JRD Merrill Specialty Equipment, Logan UT) connected to a water potential data logger (PSYPRO, Wescor Inc.) with output in μV , converted to MPa. Prior to data collection, 40 psychrometer chambers were calibrated in the laboratory using four salt solutions of known molality to generate individual calibration curves (Brown and Bartos 1982). The recorded values for all samples taken in the field were subsequently adjusted based on the slope of the calibration curve developed for the specific psychrometer.

Phloem tissue samples were taken from each study tree at a height of 1.2m on the north face of the trunk. Samples were collected between 8am and 1pm, while bole water potential was still in relative equilibrium with soil water potential. The 5 hour time window was possible because the stem is buffered to some extent from the daily change in water potential over the course of a day, as a result of ponderosa pine's capacity for stem water storage and the (near-ground) bole tissue's relatively long distance from the canopy, where xylem pressures are greatest (N. Grulke, personal communication, June 2015). Each fresh sample was immediately sealed into a psychrometer chamber and placed into a $\sim 20^\circ\text{C}$ water bath for two hours, stabilizing sample temperature. Once the samples had adequate time to equilibrate, a PSYPRO reading of the total water potential was recorded.

Resin exudation

Resin exudation on all study trees was measured once over August 4-6th using a phloem-wounding technique (Table 2). For this, a 2.5 cm diameter plug was extracted from the tree bole using a steel hole punch hammered through the cambium into the xylem at a height of 1m on the northeast side of the trunk. A spout and vial was tightly inserted into the hole, fixed in place with wood screws, and allowed to collect the releasing resin for 24 hours (Anderson 2011). Volumetric flow rate (V_R) was calculated as the volume of produced resin in ml divided by the time period in hours:

$$(4) V_R = \text{Resin (ml)} / 24 \text{ (hrs)}$$

Statistical Analysis

The purpose of this analysis was to characterize the relationship of each tree vigor response variable with the explanatory variable of CZD, accounting for other known influences. All analyses were done with R version 3.2.3 (R Core Team 2015). Sites (LM, SY) were analyzed separately for all response variables. A linear mixed model was used for this repeated measures study that incorporated multiple explanatory variables, and had both crossed and nested random effects. Crossing occurred in the study as a result of measuring all trees in all sample periods, and nesting as a result of trees occurring within neighborhoods. Crossing also occurred as a result of some measurements (SWC, PET) being repeated at the neighborhood or site level. Statistical models were checked against the assumptions of normality and equal variance. Standardized residual plots were used to check for non-constant variance, and when noted allowed to differ by neighborhood.

The fixed effect of BAL was used to account for the relationship of the study tree to surrounding tree competition in all models. Understory vegetation percent cover was part of all models as it described other sources of plant competition. SWC was included to account for water resource availability. Daily PET was include as a fixed effect to incorporate the known interactive environmental influences of solar radiation, temperature, and humidity, in the sap flow and water potential models. Through the model-fitting process it was determined that both linear and quadratic terms for CZD best characterized the fitted relationship of the response, based on residual plots and AIC model comparison. Explanatory variables were checked for collinearity for LM and SY. At LM, SWC and CZD were found to have a fairly high Pearson's correlation coefficient ($r = -0.75$), but not at SY ($r = -0.05$). For consistency in the analyses for the two sites, both factors were kept in the final model, but it is possible that this correlation may have caused variation inflation in the LM models.

All data sets were reviewed to identify potential outliers. Outliers were removed if determined to be a result of operator or mechanical error. Furthermore, a visual assessment by a plant pathologist mid-season (August 2015) revealed a dwarf mistletoe (*Arceuthobium spp.*) infestation in the trees at LM_04. This condition was considered to be significantly out of line with the conditions characterizing the rest of the trees in the study, as the dwarf mistletoe parasite extracts water and nutrients from the host tree and impacts canopy and stem growth (Hawksworth and Wiens 1996). Therefore these trees were removed from the sample for all response variables.

Fit statistics (R^2) were reported for all models. Though linear mixed-effects models cannot straightforwardly provide a value for explaining the total variance described by the model, a pseudo coefficient of determination (pseudo R^2) can be obtained (Nakagawa and Schielzeth 2013). Here this was done using the MuMIn package in R (2015). The conditional coefficients (ps R^2 c) were reported, which can be interpreted as the variance explained by both the fixed and random effects.

Sap flow

Sap flow values at each site were summed for each sample period and divided by the number of observed days, resulting in one average daily total value (kg/day) for each tree for each sample period. There were therefore 4 possible values per tree per site, or a total of 120 observations at LM and 120 observations at SY. However, mechanical failure of probes in some of the trees reduced the final number of observations to 110 at SY. For LM, mechanical failure of some probes, as well as the presence of dwarf mistletoe as previously described, also reduced the total number of observations. Once these were removed from the sample, the final number of sap flow observations at LM was 94.

The equation describing the sap flow linear mixed model is:

$$Y_{ijk} = \beta_0 + (\beta_1 * czd_{ij}) + (\beta_2 * und_{ij}) + (\beta_3 * bal_{ij}) + (\beta_4 * pet_{ik}) + (\beta_5 * swc_{ik}) + (\beta_6 * czd_{ij}^2) + \lambda_j + \omega_{ij} + \varepsilon_{ijk}$$

where

Y_{ijk} is the total average sap flow of tree j in neighborhood i at sample period k

i = neighborhood (1,2,3,4,5) j = tree (101-130) k =sample period (1,2,3,4)

β_0 is the mean average total sap flow when all explanatory variables are zero

β_1 is the change in mean average total sap flow for every 1 unit increase in competitive zone density

β_2 is the change in mean average daily total sap flow for every 1 unit increase in understory plant cover

β_3 is the change in mean average daily total sap flow for every 1 unit increase in BAL

β_4 is the change in mean average daily total sap flow for every 1 unit increase in PET

β_5 is the change in mean average daily total sap flow for every 1 unit increase in SWC

β_6 is the change in mean average daily total sap flow for every 1 unit increase in CZD²

czd_{ij} is the competitive zone density at tree j in neighborhood i

und_{ij} is the understory percent cover at tree j in neighborhood i

bal_{ij} is the proportion of basal area within a 10m radius larger than tree j in neighborhood i

pet_{ik} is the potential evapotranspiration in neighborhood i at sample period k

swc_{ik} is the volumetric soil water content in neighborhood i at sample period k

czd_{ij}^2 is the competitive zone density squared at tree j in neighborhood i

λ_j is the random effect of neighborhood i on mean average daily total sap flow, $\lambda_j \sim N(0, \sigma^2_{neighborhood})$, and λ_j and $\lambda_{j'}$ are independent.

ω_{ij} is the random effect of tree j in neighborhood i on mean average daily total sap flow, $\omega_{ij} \sim N(0, \sigma^2_{tree})$, and ω_{ij} and $\omega_{j'}$ are independent. It is assumed that λ_j and ω_{ij} are independent.

ϵ_{ijk} is the random error term for tree j on neighborhood i at time k, $\epsilon_{ij} \sim N(0, \sigma^2_{sample\ period})$, and ϵ_{ij} and $\epsilon_{j'}$ are independent. It is assumed that ϵ_{ij} , ω_{ij} , and λ_j are independent.

Water potential

Water potential was sampled twice on all trees for LM and SY, resulting in 60 observations per site. However, a faulty psychrometer reading at tree SY_03_56 in the first round of sampling reduced the total number of observations at SY to 59. Due to dwarf mistletoe, 12 more observations were dropped from the

LM sample, resulting in a total of 48. Another consideration of this analysis was the high number of explanatory variables (6) included with a relatively small sample size (48 or 59 observations). All factors were kept because they either were known drivers of water movement in trees, or because they were pertinent to addressing the research questions. However, this did reduce the power of the statistical model and increase the possibility that other data taken under the same conditions would produce different statistical results.

The equation describing the water potential linear mixed model is:

$$Y_{ijk} = \beta_0 + (\beta_1 * czd_{ij}) + (\beta_2 * und_{ij}) + (\beta_3 * bal_{ij}) + (\beta_4 * pet_{ik}) + (\beta_5 * swcl_{ik}) + (\beta_6 * czd_{ij}^2) + \lambda_j + \omega_{ij} + \epsilon_{ijk}$$

where

Y_{ijk} is the total water potential of tree j in neighborhood i at sample period k

i= neighborhood (1,2,3,4,5) j= tree (101-130) k=sample period (2,4)

β_0 is the mean total water potential when all explanatory variables are zero

β_1 is the change in mean total water potential for every 1 unit increase in competitive zone density

β_2 is the change in mean total water potential for every 1 unit increase in understory plant cover

β_3 is the change in mean total water potential for every 1 unit increase in BAL

β_4 is the change in mean total water potential for every 1 unit increase in PET

β_5 is the change in mean total water potential for every 1 unit increase in SWC

β_6 is the change in mean water potential for every 1 unit increase in CZD²

czd_{ij} is the competitive zone density at tree j in neighborhood i

und_{ij} is the understory percent cover at tree j in neighborhood i

bal_{ij} is the proportion of basal area within a 10m radius larger than tree j in neighborhood i

pet_{ik} is the potential evapotranspiration in neighborhood i at sample period k

swc_{ik} is the volumetric soil water content in neighborhood i at sample period k

czd_{ij}^2 is the competitive zone density squared at tree j in neighborhood i

λ_j is the random effect of neighborhood i on mean total sap flow, $\lambda_j \sim N(0, \sigma_{neighborhood}^2)$, and λ_j and $\lambda_{j'}$ are independent.

ω_{ij} is the random effect of tree j in neighborhood i on mean total water potential, $\omega_{ij} \sim N(0, \sigma_{tree}^2)$, and ω_{ij} and $\omega_{j'}$ are independent. It is assumed that λ_j and ω_{ij} are independent.

ϵ_{ijk} is the random error term for tree j on neighborhood i at time k , $\epsilon_{ij} \sim N(0, \sigma_{sample\ period}^2)$, and ϵ_{ij} and $\epsilon_{j'}$ are independent. It is assumed that ϵ_{ij} , ω_{ij} , and λ_j are independent.

Resin exudation

A seasonally averaged value of soil water content was used to account for the general water resource environment being experienced by the tree for resin exudation. PET was not incorporated into the resin statistical model as its relationship to resin formation was considered to be too indistinct to contribute greatly to the model. Resin exudation was sampled once on all trees for LM and SY, resulting in 30 observations at SY and 24 at LM after removal of dwarf mistletoe trees from the dataset. Similarly to the water potential analysis consideration, the high number of explanatory variables (5) included in the model with a small sample size (24 or 30 observations) may have increased the possibility that other data taken in the same conditions would produce different statistical outcomes.

The equation describing the resin exudation linear mixed model is:

$$Y_{ij} = \beta_0 + (\beta_1 * czd_{ij}) + (\beta_2 * und_{ij}) + (\beta_3 * bal_{ij}) + (\beta_5 * aswc) + (\beta_6 * czd_{ij}^2) + \lambda_j + \epsilon_{ij}$$

where

Y_{ijk} is the total resin exudation of tree j in neighborhood i

$i =$ neighborhood (1,2,3,4,5) $j =$ tree (101-130)

β_0 is the mean total resin exudation when all explanatory variables are zero

β_1 is the change in mean total resin exudation for every 1 unit increase in competitive zone density

β_2 is the change in mean total resin exudation for every 1 unit increase in understory plant cover

β_3 is the change in mean total resin exudation for every 1 unit increase in BAL

β_5 is the change in mean total resin exudation for every 1 unit increase in SWC

β_6 is the change in mean water potential for every 1 unit increase in CZD²

czd_{ij} is the competitive zone density at tree j in neighborhood i

und_{ij} is the understory percent cover at tree j in neighborhood i

bal_{ij} is the proportion of basal area within a 10m radius larger than tree j in neighborhood i

$aswc_{ik}$ is the volumetric soil water content in neighborhood i averaged over the 2015 study season

czd_{ij}^2 is the competitive zone density squared at tree j in neighborhood i

λ_j is the random effect of neighborhood i on mean total resin exudation, $\lambda_j \sim N(0, \sigma^2_{neighborhood})$, and λ_j and $\lambda_{j'}$ are independent.

ϵ_{ij} is the random error term for tree j on neighborhood i, $\epsilon_{ij} \sim N(0, \sigma^2_{tree})$, and ϵ_{ij} and $\epsilon_{i'j'}$ are independent.

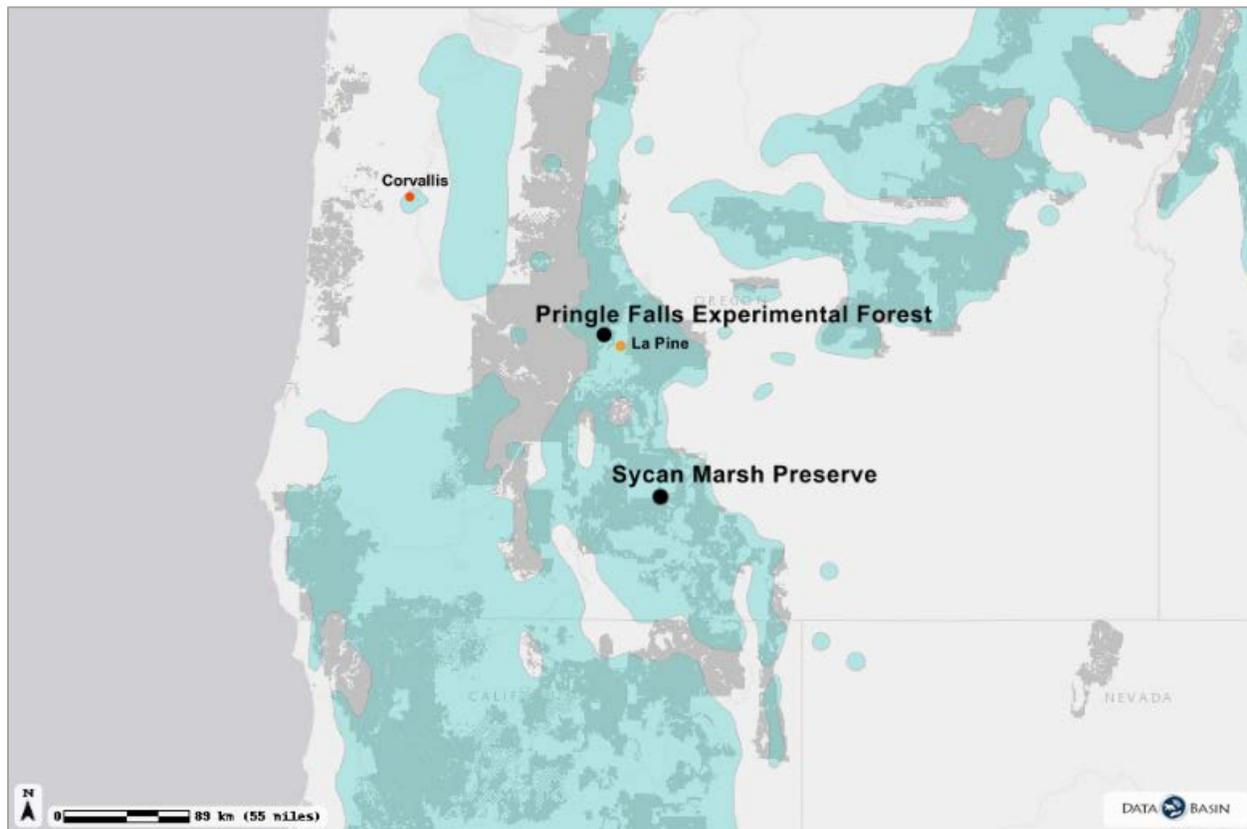


Figure 2. Locations of study sites in Oregon, USA. Lookout Mountain, located within Pringle Falls Experimental Forest (USFS) and Sycan Marsh Preserve (The Nature Conservancy). Blue polygons indicate ponderosa pine distribution. Grey polygons indicate US Forest Service ownerships. Credit: databasin.org

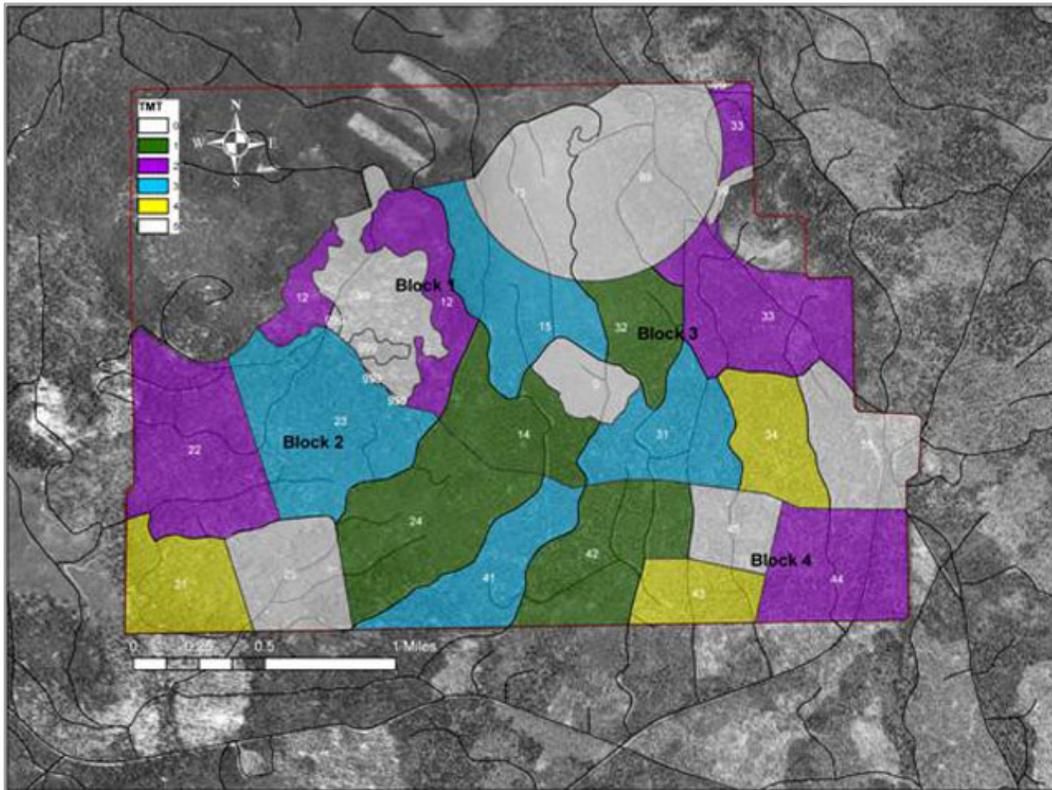


Figure 3. Original randomized block design for silvicultural treatment study in the Lookout Mountain Unit of Pringle Falls Experimental Forest, Oregon (USFS). Study areas (neighborhoods) were selected from Block 2 only, as timing of thinning and burning treatments fit best with the objective of looking at trees after recent treatment.

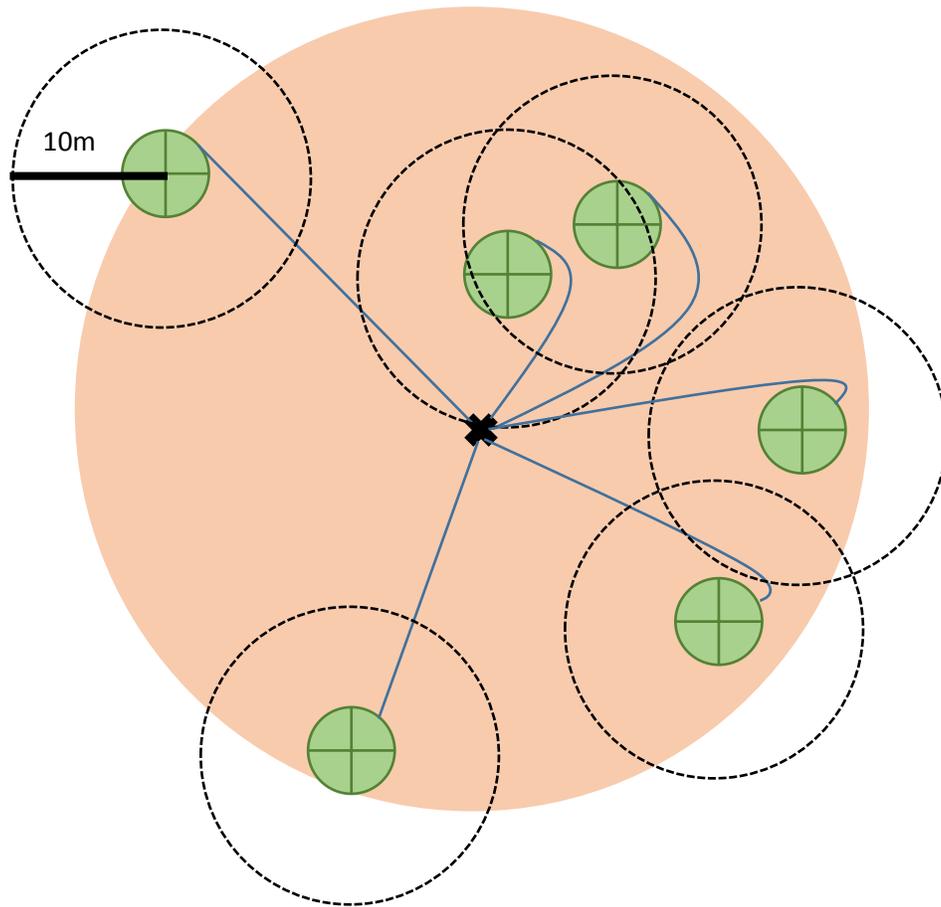
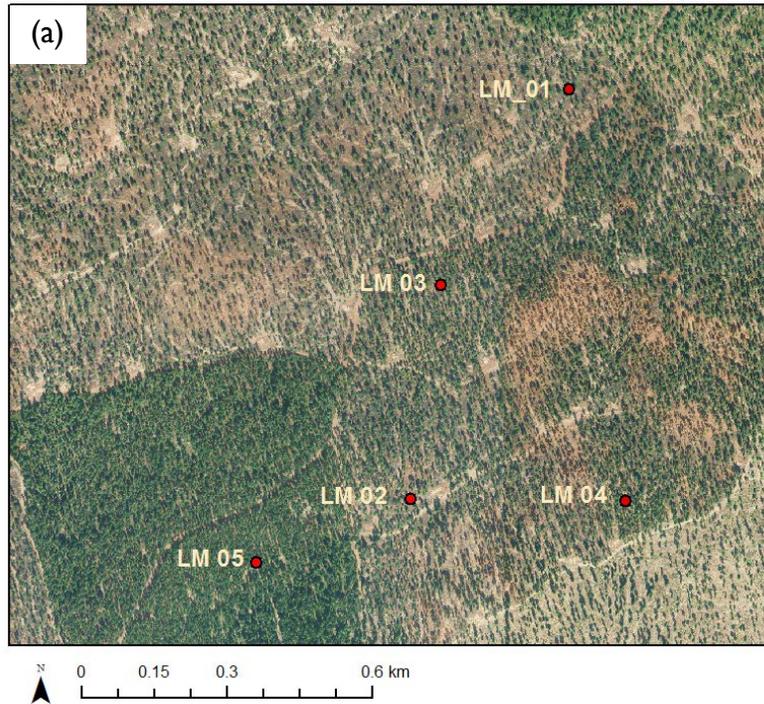


Figure 4. Sample depiction of neighborhood layout used to observe sap flow at Lookout Mountain and Sycan Marsh in south-central OR in 2015 (not to scale). Approximate neighborhood extent represented by light-red circle. Green crosshair circles represent selected dominant or co-dominant ponderosa pines for study. The blue lines depict the 30 m max-length cables that connected sap flow probes to the data logger, shown as the black center x. The dotted lines around each study tree represent its 10m fixed plot, or zone of competitive influence.

Lookout Mountain neighborhoods



Sycan Marsh neighborhoods

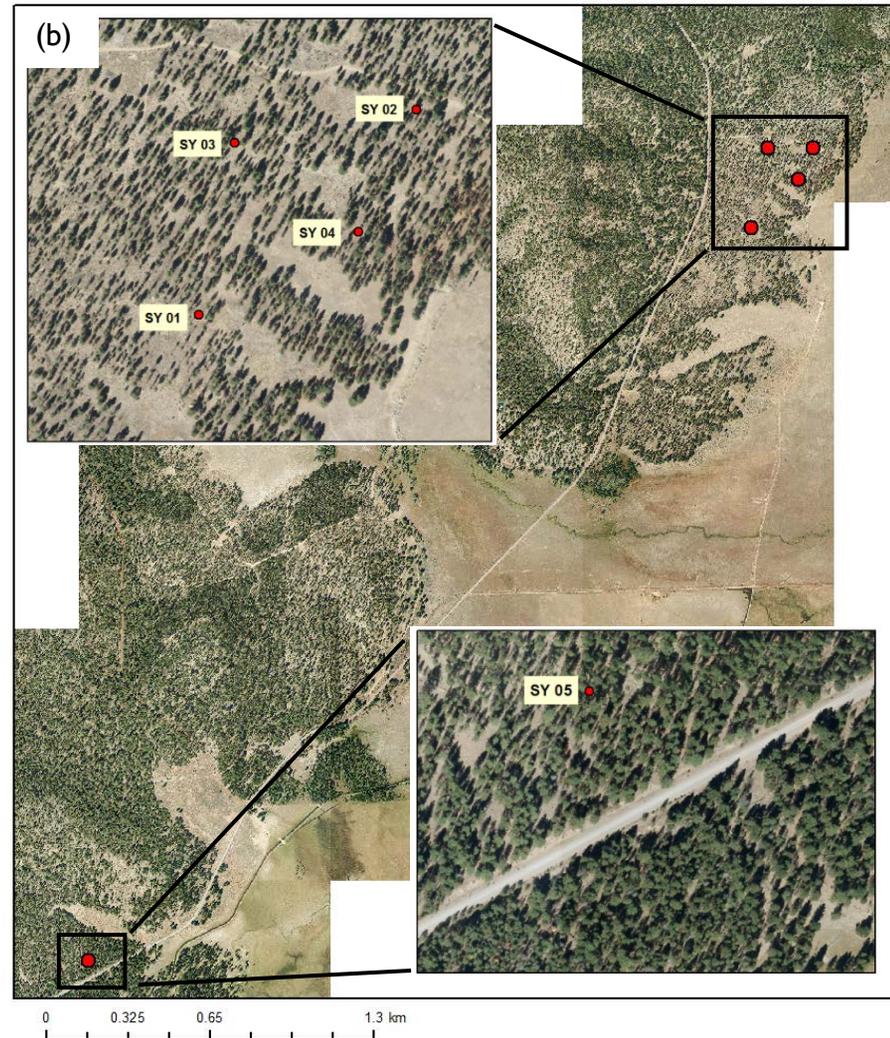


Figure 5. Approximate neighborhood locations at (a) Lookout Mountain and (b) Sycan Marsh study sites. Neighborhood GPS locations were randomly generated after stratifying each site area into 5 levels of tree density (in trees per acre). Neighborhoods indicated by red points and labeled (01 – 05) in order of ascending estimated density.

Table 1. Sap flow data collection sampling periods for June – October 2015 at Lookout Mountain (LM) and Sycan Marsh (SY) study sites in south-central OR. Each rotation within each sample period designated by a or b. Note: Due to malfunctioning data loggers, LM 03 and LM 01 sampling data from closest time available to the sampling period was used for rotations 3a and 4a, respectively.

Sap flow sample period	Neighborhoods	Start date	End date
1a	LM 01, 03, 05 SY 01, 03 ,05	30-Jun	5-Jul
1b	LM 02, 04, 05 SY 02, 04, 05	8-Jul	13-Jul
2a	LM 01, 03, 05 SY 01, 03 ,05	20-Jul	25-Jul
2b	LM 02, 04, 05 SY 02, 04, 05	5-Aug	10-Aug
3a*	LM 03	25-Aug	30-Aug
3a	LM 01, 05 SY 01, 03 ,05	1-Sep	6-Sep
3b	LM 02, 04, 05 SY 02, 04, 05	11-Sep	16-Sep
4a*	LM 01	21-Sep	22-Sep
4a	LM 03, 05 SY 01, 03 ,05	24-Sep	29-Sep
4b	LM 02, 04, 05 SY 02, 04, 05	2-Oct	7-Oct

1 day = 0:00-23:55 or 0:10-24:00
*off-set due to data logger malfunction

Table 2. Sampling dates at Lookout Mountain and Sycan Marsh study sites in south-central OR compared to sap flow sample periods for soil moisture (SWC), water potential, and resin exudation over June – October 2015 season.

Sap flow				
sample period	date range	soil water content (SWC)	water potential	resin exudation
1	06/30 – 07/13	07/06 – 07/07	-	-
2	07/21 – 08/10	07/28 – 07/29	07/25 – 07/26	08/04 – 08/06
3	09/01 – 09/16	09/07– 09/08	-	-
4	09/24 – 10/07	09/29 – 10/01	09/24 – 09/25	-

CHAPTER 5 - RESULTS

Environmental influences: Soil moisture, PET

Averaged volumetric soil water content (SWC) readings (0-50 cm for canopy and gap) declined over the course of the season at both LM and SY (Figure 6). Rate of decline for the season was equivalent across all neighborhoods by site. However, SWC for all neighborhoods was generally 10% lower at LM than at SY by mid-August. LM 05, the neighborhood with the highest CZD level at that site, exhibited an asymptotic minimum in SWC from late-July that was not seen in SY until early September. For all neighborhoods, where asymptotic minimums occurred, they were substantially lower and reached earlier at LM. For LM, average soil moisture trends were within a range of 0.1 m³/m³ of each other for LM 01- LM 05. SY 01, 02, 03 and 05 showed similar soil moisture values; SY 04, however, was higher by at least 0.04 m³/m³ than the other neighborhoods for the entire season. SY 04's position nearer to the seasonal wetland zone of the Preserve may have influenced its moisture profile. PET demonstrated a declining seasonal trend (Figure 7), fairly similar in range and pattern at both weather stations, with values between 4-6mm for the majority of the June-August period. PET dropped off to a general range of 2-4mm thereafter.

Seasonal soil moisture and sap flow observations at both sites over the season indicated a linear relationship between the two variables (Figure 8a), though the variability of sap flow increased greatly as soil moisture increased. With more available moisture also comes a higher capacity for sap flow movement, but this capacity is dependent on other circumstances of the tree and its growing conditions, as the increase in variability may have indicated. Visual comparison of soil moisture and water potential at both LM and SY showed a slight positive trend (Figure 9a). For resin exudation, a seasonal average of soil moisture was used to compare the variables, but little relationship was discerned: the range of resin produced was similar despite relative soil moisture status for a given tree (Figure 10a). Graphic comparisons of PET showed little direct correlation for average daily sap flow or water potential (Figures 8b-9b).

Competitive influences: CZD, Neighborhood scale density, understory

The ranges of competitive zone density (CZD), neighborhood density (averaged values of prism-estimated basal area at each study tree), understory vegetation cover estimates by neighborhood, and average study tree dbh were all found to cover a wider range of values at LM compared to SY (Table 3, Figures 11 - 12). CZD values were also more evenly distributed across the range of possible values at LM than at SY (Figure 12a).

CZD values for LM ranged from 0 – 67.5 m²/ha by tree. Average tree densities at the neighborhood scale were within 8.8m²/ha of each other for LM 01, 02, 03, and 04, with a significant density increase of about 20m²/ha at LM 05. Understory cover spanned 13.67– 64.5%, and predominant species were *Chrysopsis chrysophylla*, *Ceanothus velutinus*, *Carex rossii*, and *Arctostaphylos nevadensis*. At SY, CZD values ranged from 5.2 – 37.4 m²/ha by tree, and average tree basal area at the neighborhood scale were within 4.27 m²/ha for SY 01, 02, 03, and 04, with a tree density increase of about 28 m²/ha. SY understory cover ranged from 45.67 -67%, with *Ericameria nauseosa*, *Artemisia tridentata*, *Lupinus caudatus*, and grass spp. primarily forming the understory community.

Diameter variation (dbh) among the six study trees comprising each neighborhood was inconsistent across LM neighborhoods (Figure 11a). Average dbh declined from LM_01 to LM_05, and was especially reduced in range and size at LM_05. This was the inverse of CZD values at LM, which generally increased from LM_01 – LM_05. Therefore, for LM, where tree competition was the highest, the size of the monitored trees was also the smallest, which could indicate that some degree of confounding existed between the two factors in explaining either's relationship with a given response variable. For SY, dbh range and distribution across neighborhoods was more even. However, the overall extent of dbh was narrower at SY than at LM. Trees at SY spanned approximately 30 - 60 cm, while at LM the range was ~ 50 – 100 cm. Overall, trees were found to be bigger and to have more variable competitive status at LM, but trees were smallest where competition was greatest. SY had a narrower range of CZD and more uniform tree diameters. These inconsistencies were a result of the conditions available to sample at each site.

BAL, calculated to better understand the size of each study tree in relation to its local tree competition, varied differently between LM and SY, as well as by neighborhood within each site (Figure 12b). All study trees at neighborhoods LM_05 and SY_05 were larger in basal area than over half of the other trees within a 10m radius. These were also the trees experiencing the highest CZDs. This fit with the study design objective to select dominant or co-dominant trees. If there was little surrounding competition, it was more likely that it would be from trees in the same size class as the study tree. If there was more competition, then the likelihood rose that these trees were smaller than the tree of interest. There was more variation in BAL for the other neighborhoods, reflecting the secondary objective to choose trees in a range of competitive arrangements (single, paired, clumped). The exception to this was LM_01, where the residual density was so low that all study trees were more than 10m away from the next nearest tree.

Sap flow

At both LM and SY, average total daily sap flow decreased over the course of the season, corresponding with the decline in SWC and PET at both sites (Figure 8). At LM average total sap flow values for the 2015 season, when examined graphically, increased in variation and upper amount as CZD increased, up to approximately 40 m²/ha (Figure 13). Above this CZD threshold daily sap flow decreased in amount and variation, changing from a range of roughly 0-210 kg/day at 32.7 m²/ha down to a range of 0-15 kg/day after 40 m²/ha. This shift in variation and amount is consistent across each sampling period at LM. Examination of the mean average daily total sap flow data in conjunction with other possible influences – tree age, understory percent cover and BAL - did not reveal an explanation for the variation in sap flow observed for CZDs of <40 m²/ha. At SY, mean average total sap flow values did not exhibit a clear relationship to CZD when examined graphically (Figure 14). Sap flow values were similar across all trees from 5.2 – 37.4 m²/ha, spanning a range of 0 - 130 kg/day. For the highest CZDs at SY, some of the highest sap flow values also occurred, causing a slight positive trend in sap flow with increasing CZD. The upper limit of sap flow and CZD generally corresponded with the same CZD for the highest sap flow values at LM.

Across three sample periods, the upper limits of the sap flow range was higher at LM than at SY for the majority of observations, except for SY 05 in period 1. The higher sap flow at LM stood in contrast to the comparatively lower soil moisture readings at all LM neighborhoods versus SY. Trees at similar CZDs in each site also reflected this difference. For example, at 9.7 m²/ha, average total sap flow values for tree LM_03_106 were: 81.91, 62.09, 39.38, and 15.40 kg/day. Soil moisture at LM_03 at each sap flow sample period was 0.071, 0.092, 0.045 and 0.065 m³/m³. Sap flow values for tree SY_01_136, also with a CZD of 9.7m²/ha, were half or less: 48.62, 15.95, 5.96, and 8.46 kg/day, even though soil moisture values in that neighborhood were 0.152, 0.152, 0.09 and 0.119 m³/m³.

Results of a marginal t-test for LM showed statistically significant evidence of a relationship between mean average daily total sap flow and each of the variables of CZD and SWC after accounting for the other explanatory variables in the model (Table 4, Figure 15a). Note that the comparatively smaller tree sizes at the upper end of the CZD range at LM may have contributed to the distinct decline in sap flow rates and subsequent statistical result, given that a diameter-dependent measure (sapwood area) is inherent in the calculation for sap flow. The SY data did not provide evidence of a statistically significant relationship between mean average total sap flow and the competition-based variables of CZD, understory or BAL, nor for the environmental drivers of soil moisture or PET, after accounting for the other variables in the model

(Table 4, Figure 15b). In part, this may have been a consequence of the comparatively limited range covered by the explanatory variable of CZD at SY: its range was only about half as wide as the CZD range at LM. This could have constricted the ability to see potential relationships between these variables. Soil moisture was also higher at SY, which may have reduced tree water stress overall at the site, also obscuring possible relationships between competition and sap flow.

Water potential

Visual analysis of the water potential data indicated that a decline in average neighborhood SWC at LM or SY corresponded with a decline in water potential for approximately half of the study trees (Figure 16 and 17). Water potential did not show a clear trend with CZD or neighborhood at either site in either sample period. SWC at LM declined by an average of 20% from late July to late September; however, only 14 trees (half the sample) across all neighborhoods experienced a decrease in water potential over 0.3 MPa. A 0.3 MPa change was less than 10% of the total range of water potentials observed in the sample. Across all study trees at LM, mean values for water potential were -1.28 MPa and -1.54 MPa in July and September, respectively. Eleven trees experienced little change and five trees showed an increase over 0.3 MPa. At SY, volumetric soil moisture declined by an average of 8% from late July to late September. Across all study trees at SY, tree water potential averaged -1.23 MPa and -1.81 MPa in July and September, respectively. Eighteen trees showed a negative change in water potential over 0.3 MPa, ten showed little change, and one tree increased more than 0.3 MPa from the first to second reading. Despite higher SWC over the season, a lower rate of soil moisture decline, and CZD values over a smaller range, trees sampled at SY had a greater average decline in water potential from the middle to the near-end of the 2015 summer season than the trees sampled at LM. This indicates that LM study tree water status was generally less affected by a decline in available water resources than the trees at SY, even when the decline was 12% greater at LM. At both sites more than half of the trees maintained bole water potentials greater than -1.8 MPa over the season, while a third dropped below -2.0 MPa by late-September, a putative leaf-water potential threshold for [total?] stomatal closure in leaf water potentials (Martínez-Vilalta et al. 2004). Given that water potentials are generally lower in the canopy than in the bole, the number of trees experiencing moisture stress is likely to have been greater.

Evidence of a statistically significant relationship was shown at LM between mean water potential and CZD after accounting for understory cover, BAL, SWC and PET (Table 5, Figure 15a). For SY, there was no evidence of a statistically significant relationship between mean water potential and CZD, and neither were

statistically significant relationships found for mean water potential with the other explanatory variables (Table 5, Figure 15b).

Resin exudation

Visual examination of the raw resin exudation data did not reveal a clear trend between CZD and the volume of resin produced by the trees in this study (Figures 18-19). Resin exudation reached higher upper amounts at LM than at SY when looked across the entire range of CZD (Figure 20). The bigger trees at LM produced a range of 0 – 36 ml/day versus 0 – 16.5 ml/day at SY. In general resin exudation increased with dbh (Figure 21). However, several trees did not produce any resin at all in 24 hours; 7 trees at LM and two at SY had zero results, with two more only producing 0.5 ml/day.

The slope of the regression lines for resin exudation were notably different at each site. At LM a negative trend was shown by the data, but for SY a hyperbolic relationship was apparent. The discrepancy in these trends is difficult to account for, but may be related to the more restricted CZD and tree size range from LM to SY as previously described. A larger sample size may also have helped to more accurately estimate these relationships. No statistically significant relationship was found between mean resin exudation and CZD at LM or SY after accounting for the other explanatory variables in the model, nor for any of the other variables (Table 6, Figure 15a & 15b).

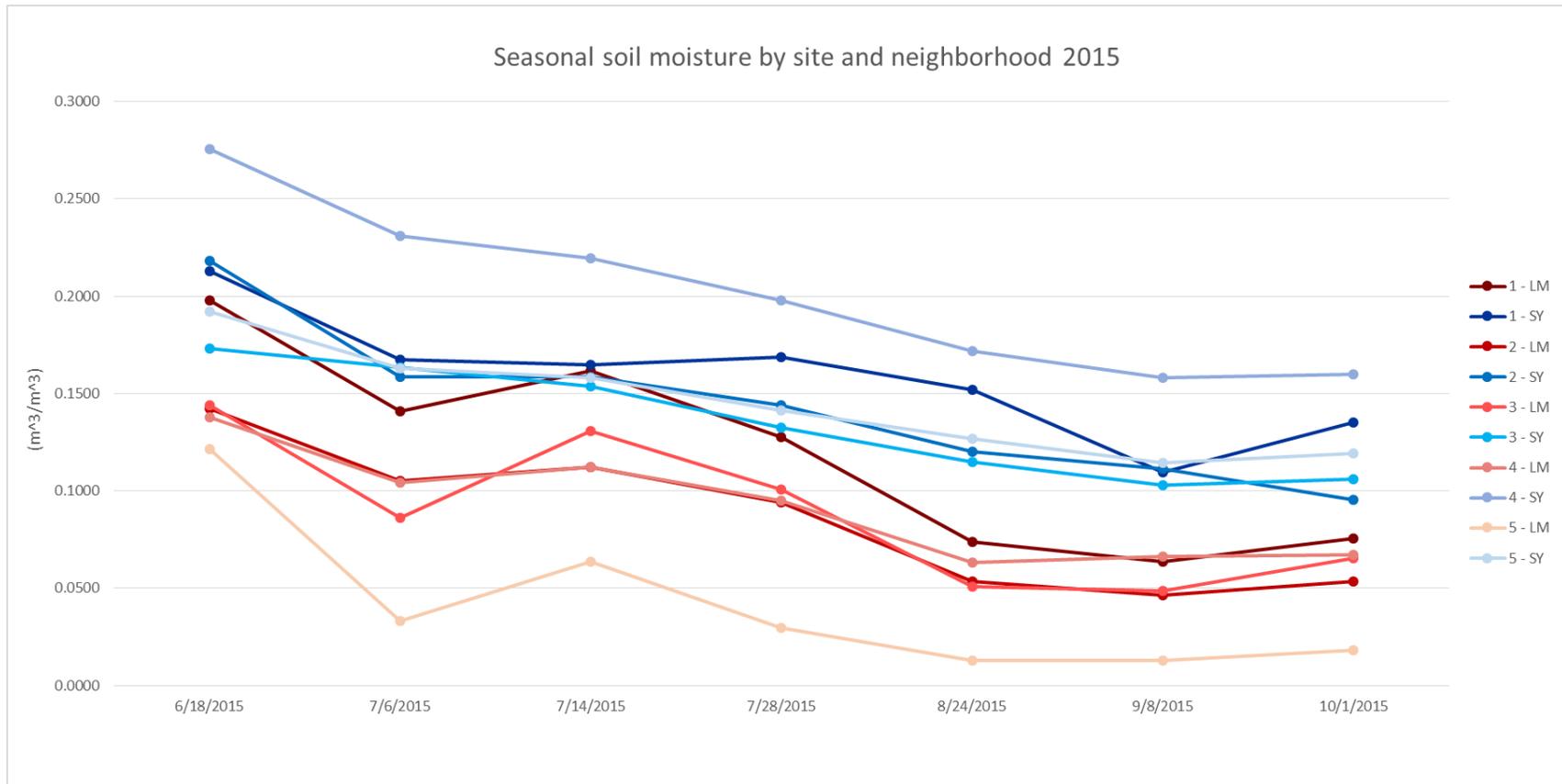


Figure 6. Soil moisture trends (weighted average of 0-50 cm measurements) by site and neighborhood from mid-June to beginning of October 2015 for Lookout Mountain (LM) and Sycan Marsh (SY) in south-central Oregon. Seven measurement dates used to characterize the change in soil water content (m^3/m^3) over the season. Each line represents values by site (LM, SY) and neighborhood (1,2,3,4,5). Red = LM Blue = SY.

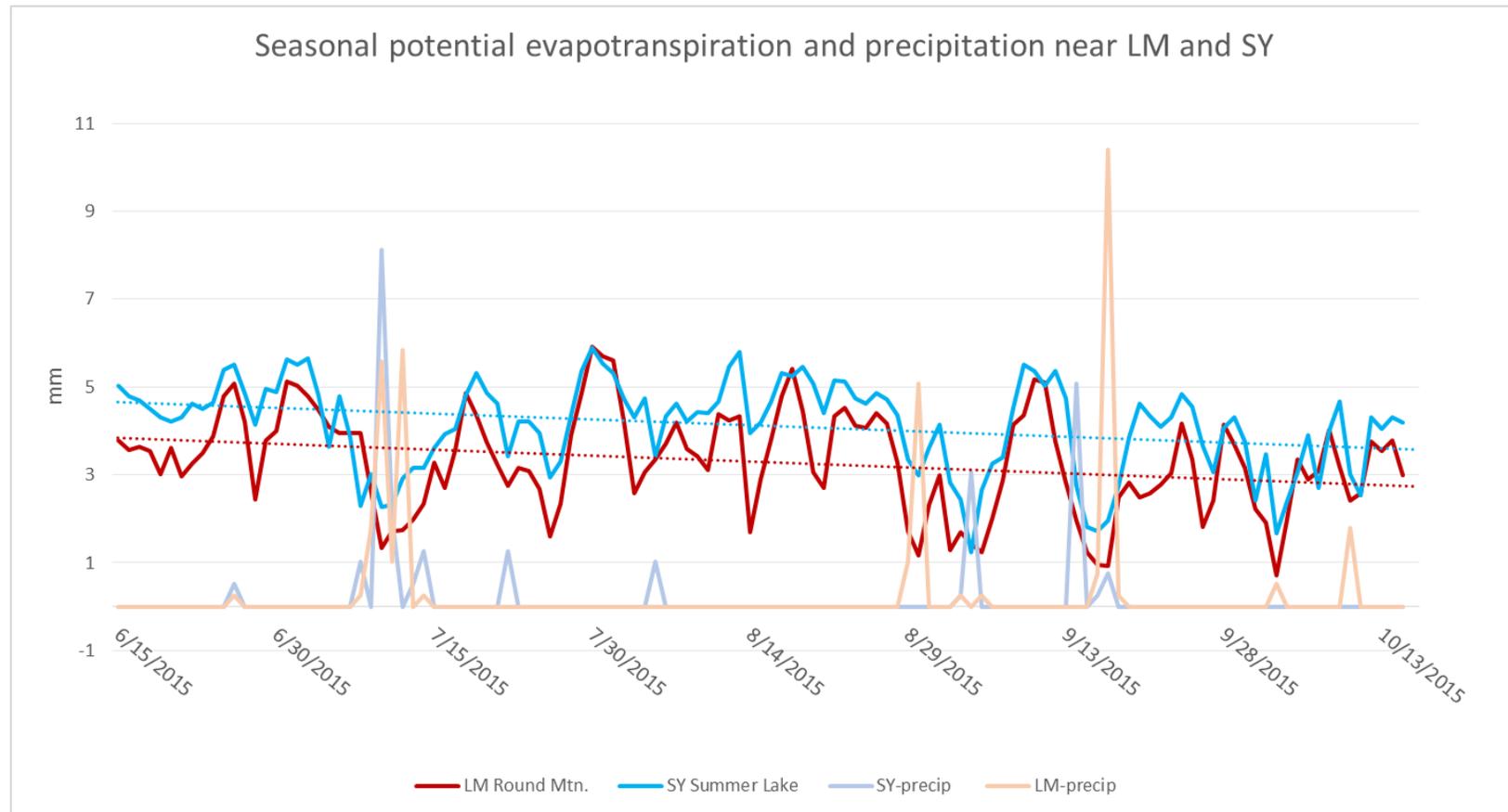


Figure 7. Oregon RAWS daily potential evapotranspiration and precipitation data recorded at weather stations adjacent to study sites: the Round Mountain RAWS near Lookout Mountain (LM) and the Summer Lake RAWS near Sycan Marsh (SY). Data shown from mid-June to mid-October 2015, covering the extent of the sampling season. Seasonal PET trends for each station represented by simple linear regression (dotted line). Red = LM Blue = SY.

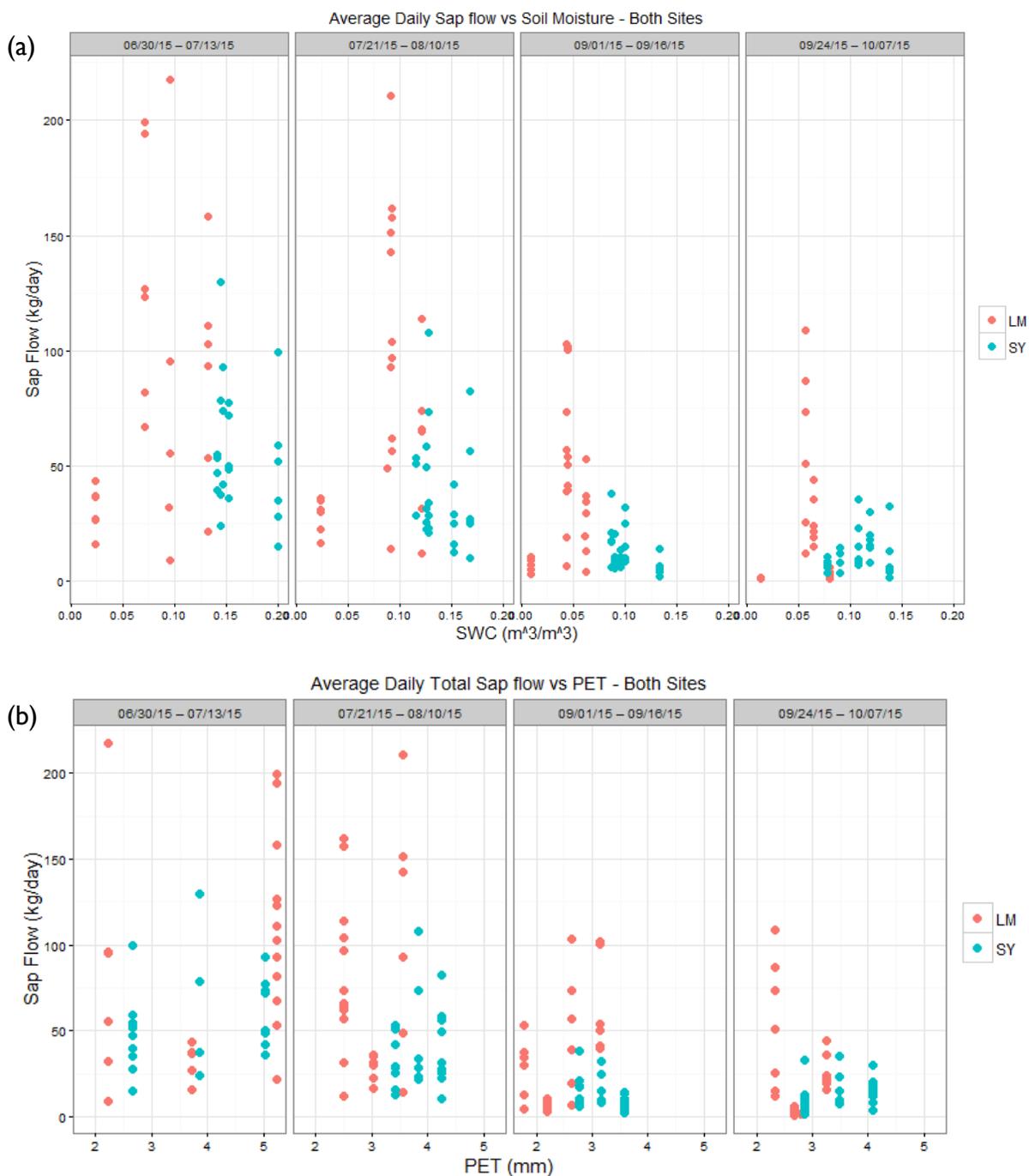


Figure 8. Sapflow in relation to evaporative demand and soil water at Lookout Mountain (LM) and Sycan Marsh (SY). (a) Volumetric soil moisture and average daily sap flow relationships for sampled mature ponderosa pines at LM and SY. (b) Potential evapotranspiration and average daily sap flow relationships at LM and SY. Each sap flow sampling period (1,2,3,4) shown separately. All trees at LM 04 removed due to presence of dwarf mistletoe. $n=24$ (LM), 30 (SY) by site and sample period. Red = LM Blue = SY.

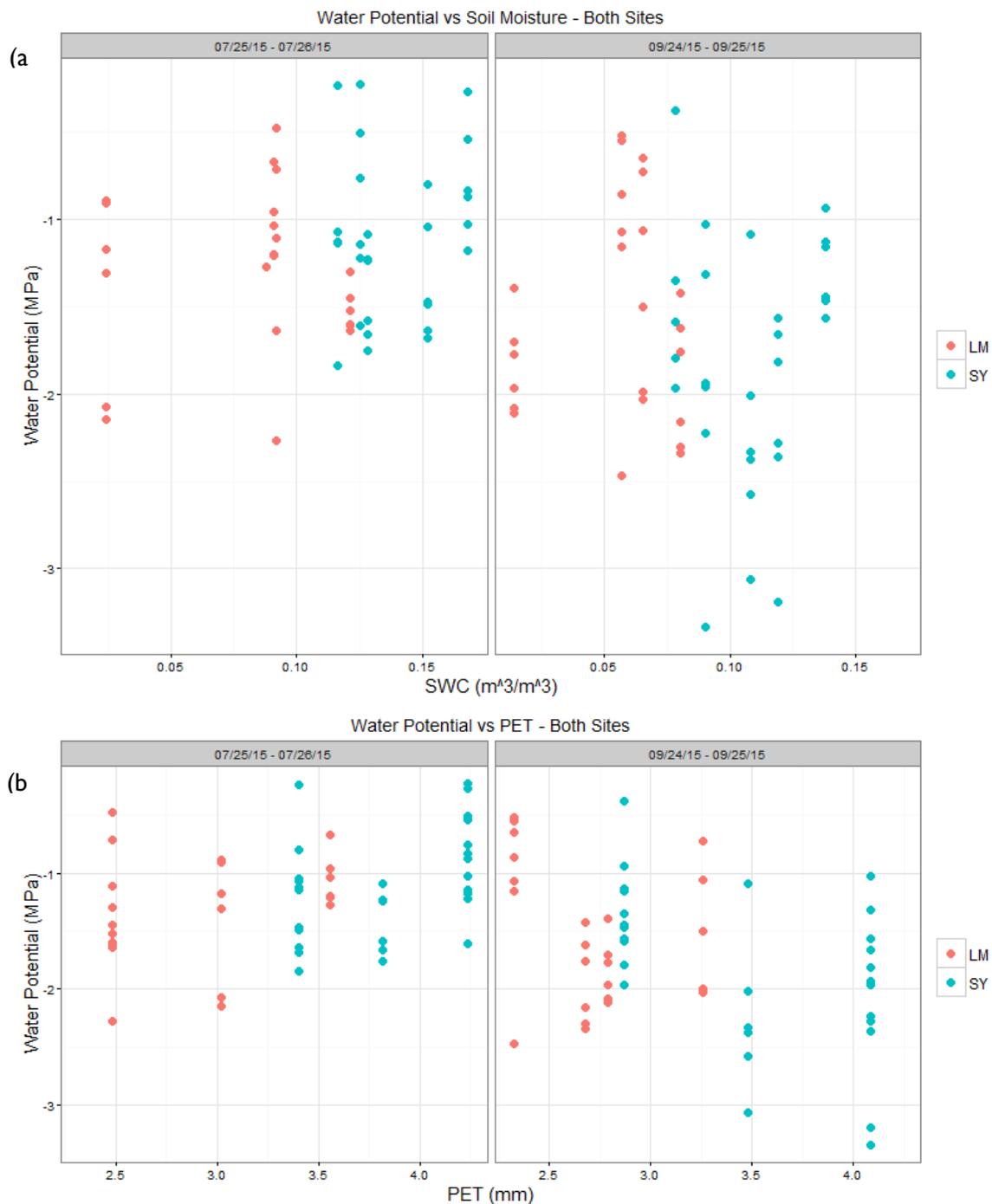


Figure 9. Relationship of environmental variables to water potential at Lookout Mountain (LM) and Sycan Marsh (SY). (a) Volumetric soil moisture and water potential relationships for sampled mature ponderosa pines at LM and SY. (b) Potential evapotranspiration (PET) and water potential relationships at LM and SY. Each sampling period shown separately. Sampling period notation (2,4) based on sap flow sample periods. All trees at LM 04 removed due to presence of dwarf mistletoe. n=24 (LM), 30 (SY) by site and sample period. Red = LM Blue = SY.

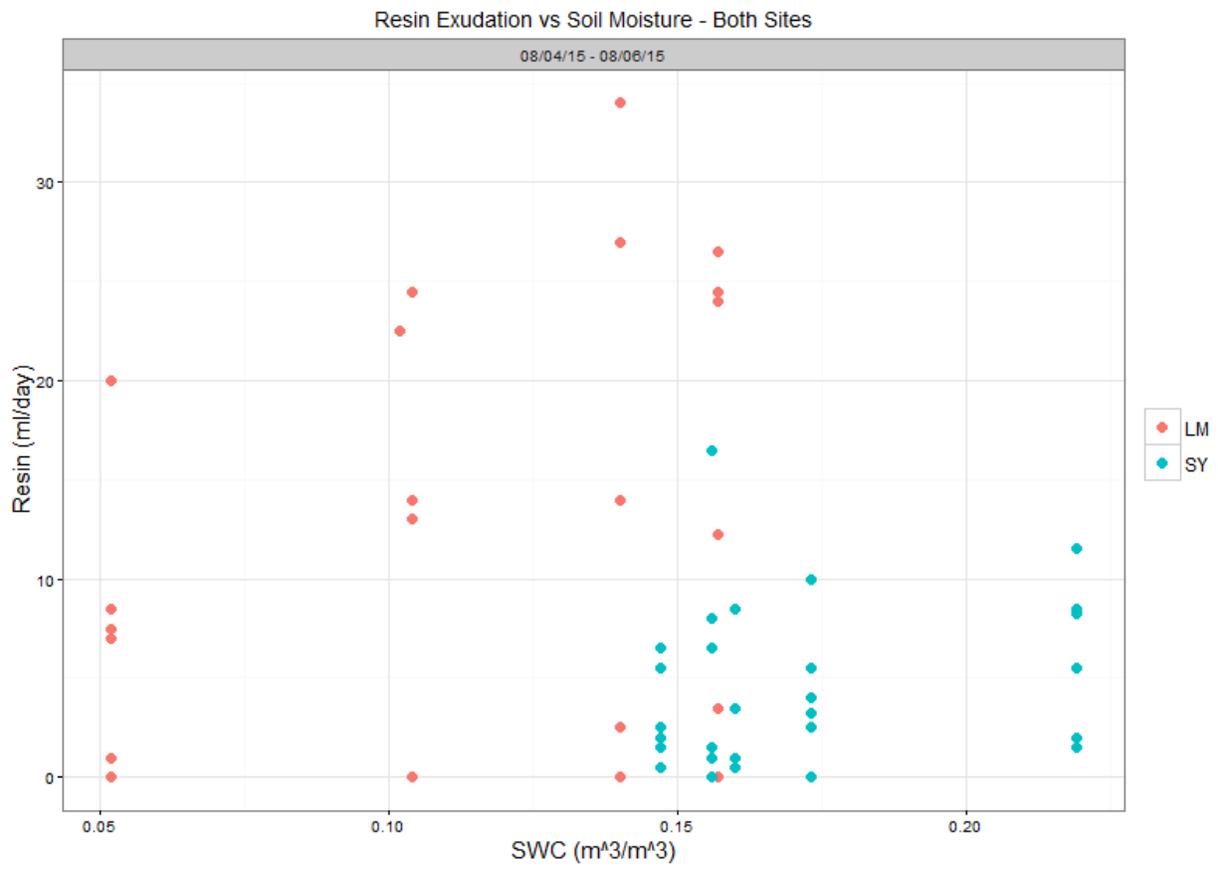


Figure 10. Volumetric soil moisture and resin exudation relationships for sampled mature ponderosa pines at Lookout Mtn. (LM) and Sycan Marsh (SY). Sampling period notation (2) based on sap flow sample periods. All trees at LM 04 removed due to presence of dwarf mistletoe. n=24 (LM), 30 (SY). Red = LM Blue = SY.

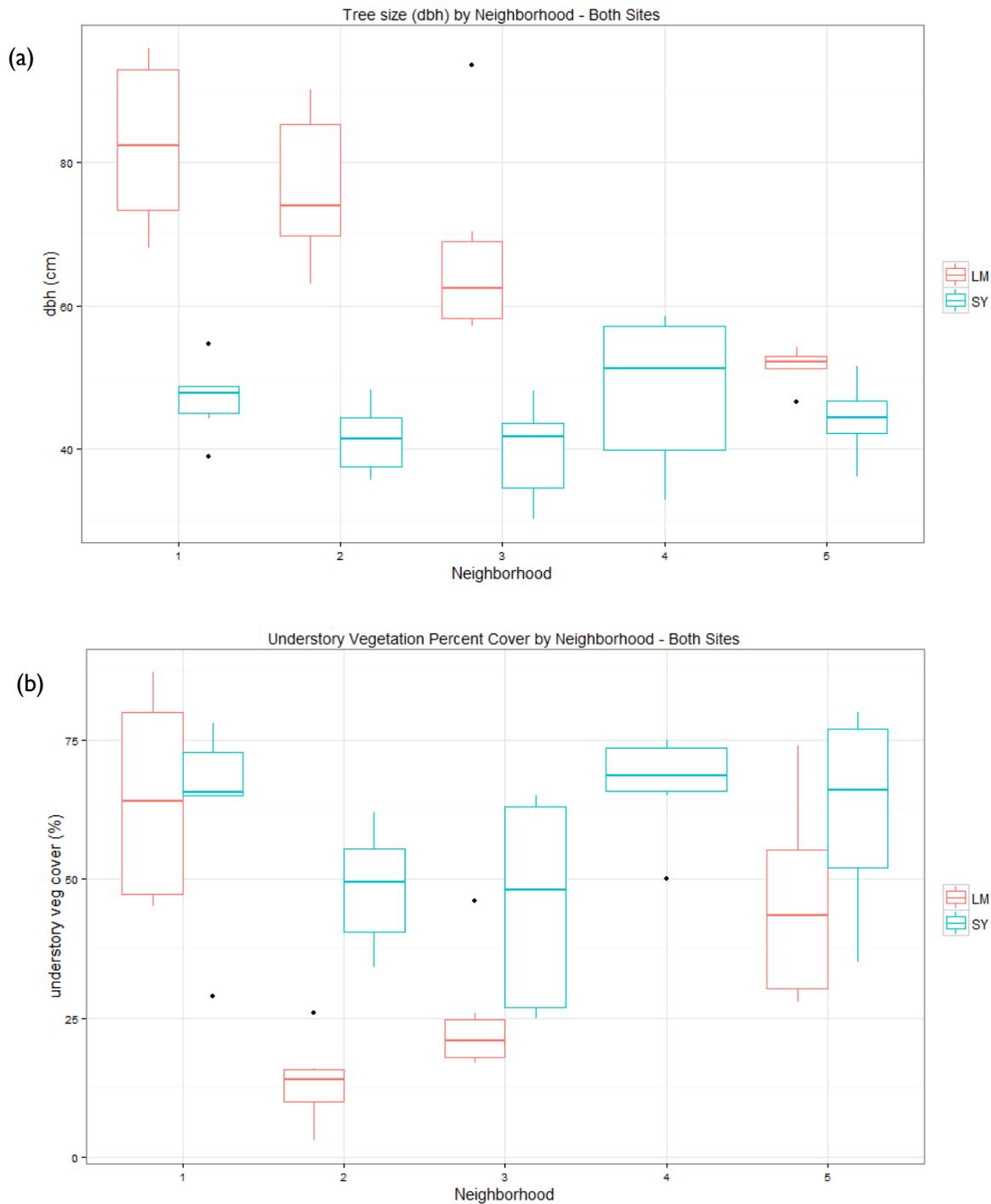


Figure 11. Range in tree size and understory percent cover present at Lookout Mountain (LM) and Sycan Marsh (SY). (a) Tree size (dbh in cm) of study trees, and (b) understory vegetation percent cover estimates, at LM and SY by neighborhood. All trees at LM 04 removed due to presence of dwarf mistletoe. n= 6 trees per neighborhood. Red = LM Blue = SY.

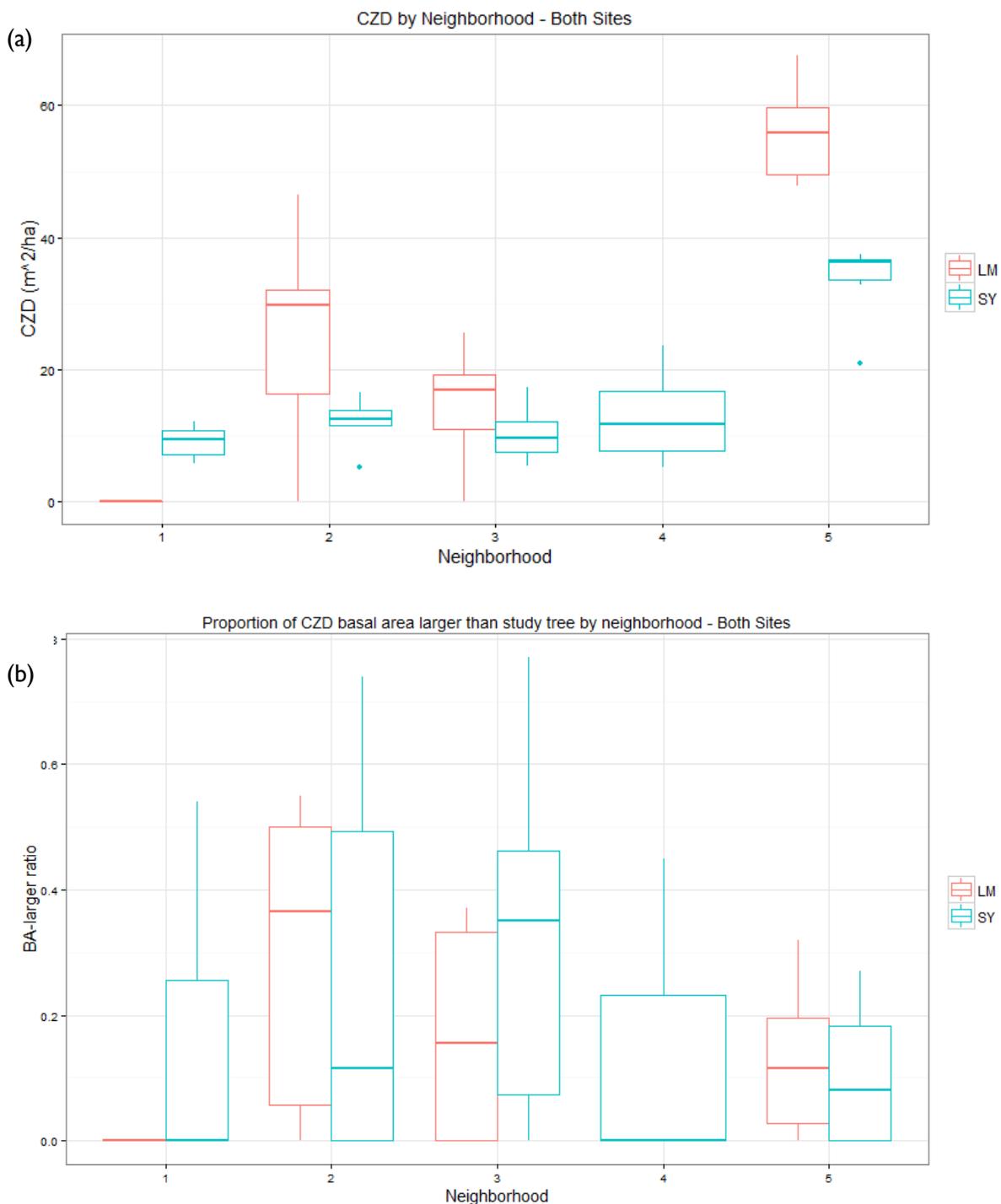


Figure 12. Range in competitive zone density (CZD) and proportion of CZD basal area that larger than study tree basal area (BAL) present at Lookout Mountain (LM) and Sycan Marsh (SY). (a) CZD in m²/ha for each study tree, and (b) BAL, at both sites by neighborhood. n= 6 trees per neighborhood. All trees at LM 04 removed due to presence of dwarf mistletoe. Red = LM Blue = SY.

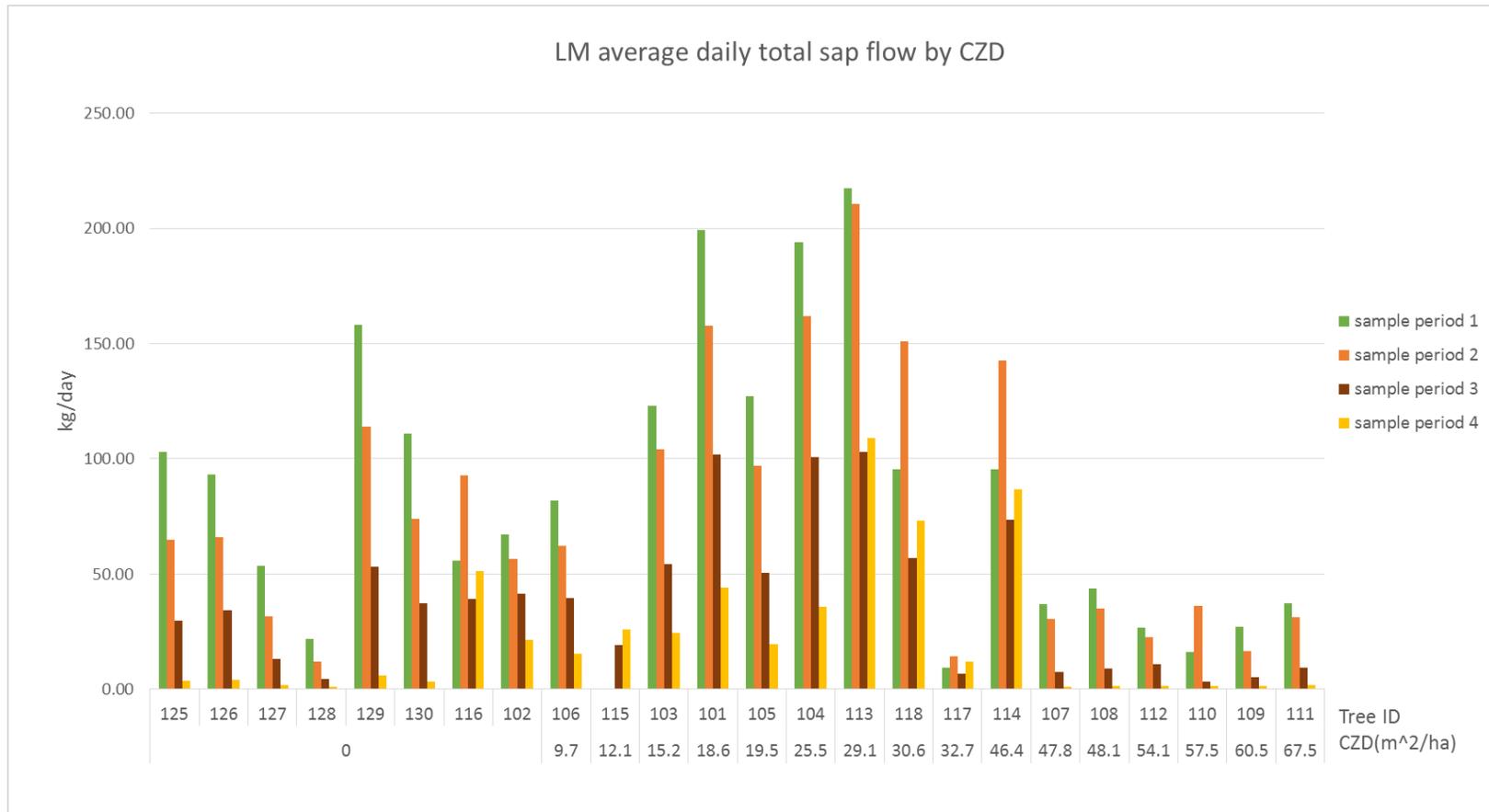


Figure 13. Average daily total sap flow for all mature ponderosa pines sampled at Lookout Mountain (LM) in south-central OR. Values in ascending order by competitive zone density (CZD). Color indicates sample period of measurement: green = 1, orange = 2, maroon = 3, and yellow = 4. Missing values at LM_115 were due to sensor malfunction. Trees LM_119, 120, 121, 122, 123 and 124 were removed from the dataset due to presence of dwarf mistletoe. $n=94$.

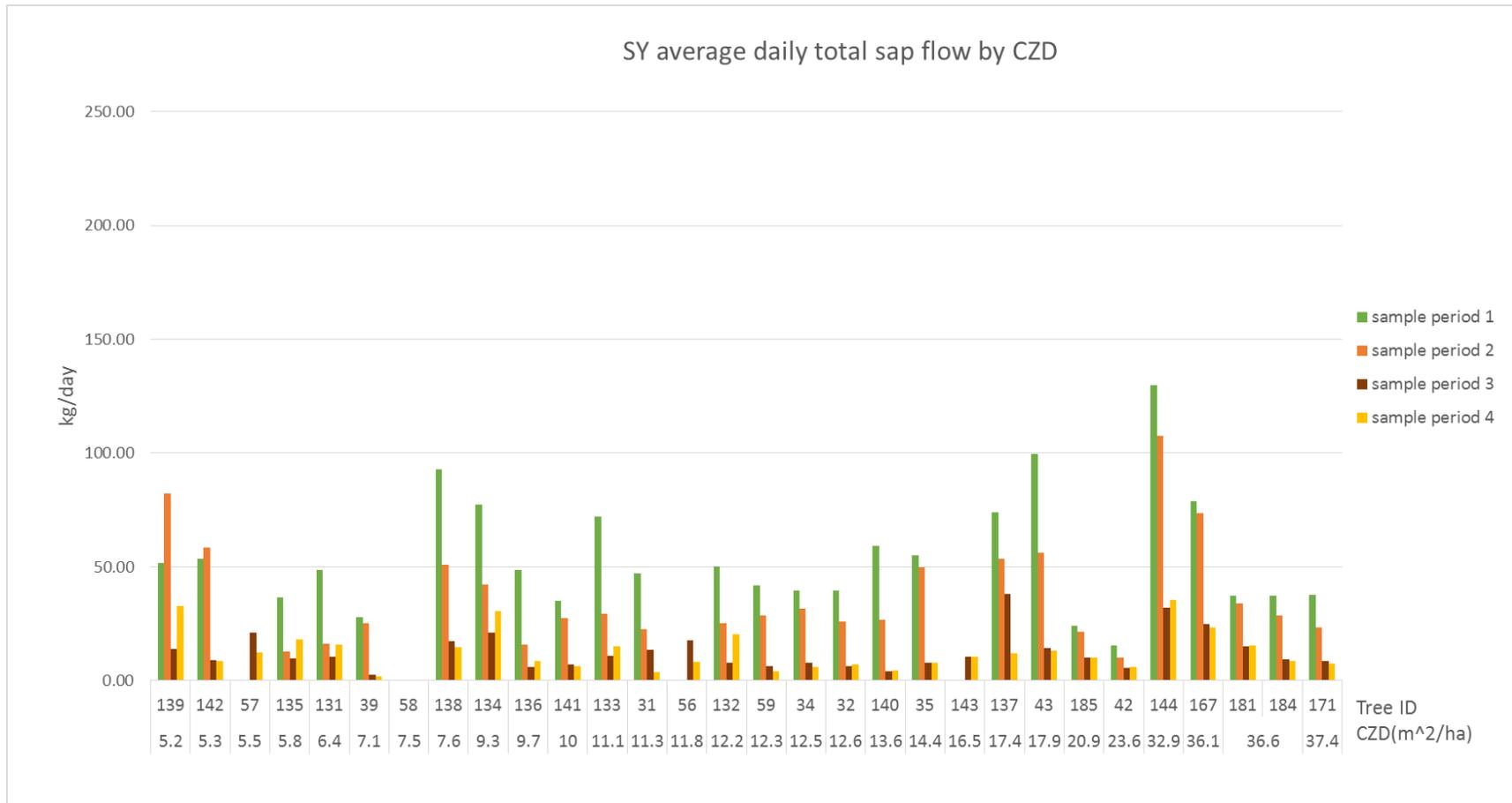


Figure 14. Average daily total sap flow for all mature ponderosa pines sampled at Sycan Marsh (SY) in south-central OR. Values in ascending order by competitive zone density (CZD). Color indicates sample period of measurement: green = 1, orange = 2, maroon = 3, and yellow = 4. Missing values at SY_57, SY_58, SY_56, and SY_143 were due to sensor malfunction. n=110.

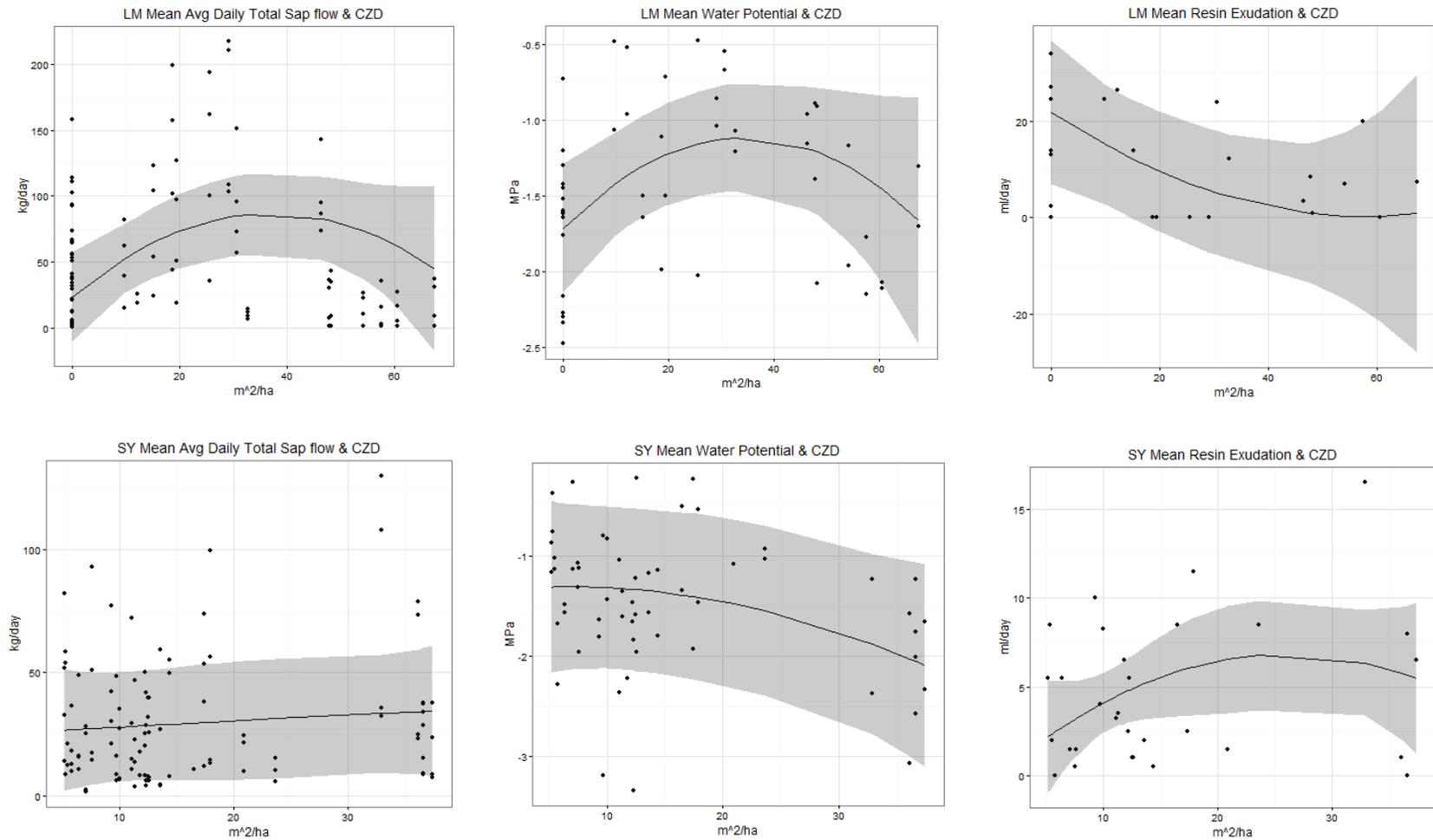


Figure 15. Regression analyses showing the estimated relationship between competitive zone density (CZD, m^2/ha) and the mean of each response variable (average daily total sap flow, water potential and resin exudation) by site for the 2015 season. Each fitted line accounts for the influences of understory percent cover, soil moisture, proportion of CZD basal area larger than study tree basal area, and potential evapotranspiration (PET excluded for resin exudation). Raw data values plotted as points, with all explanatory variables in the model except for CZD kept to the mean. 95% confidence intervals shown by grey bands. (a) Lookout Mountain (LM). (b) Sycan Marsh (SY).

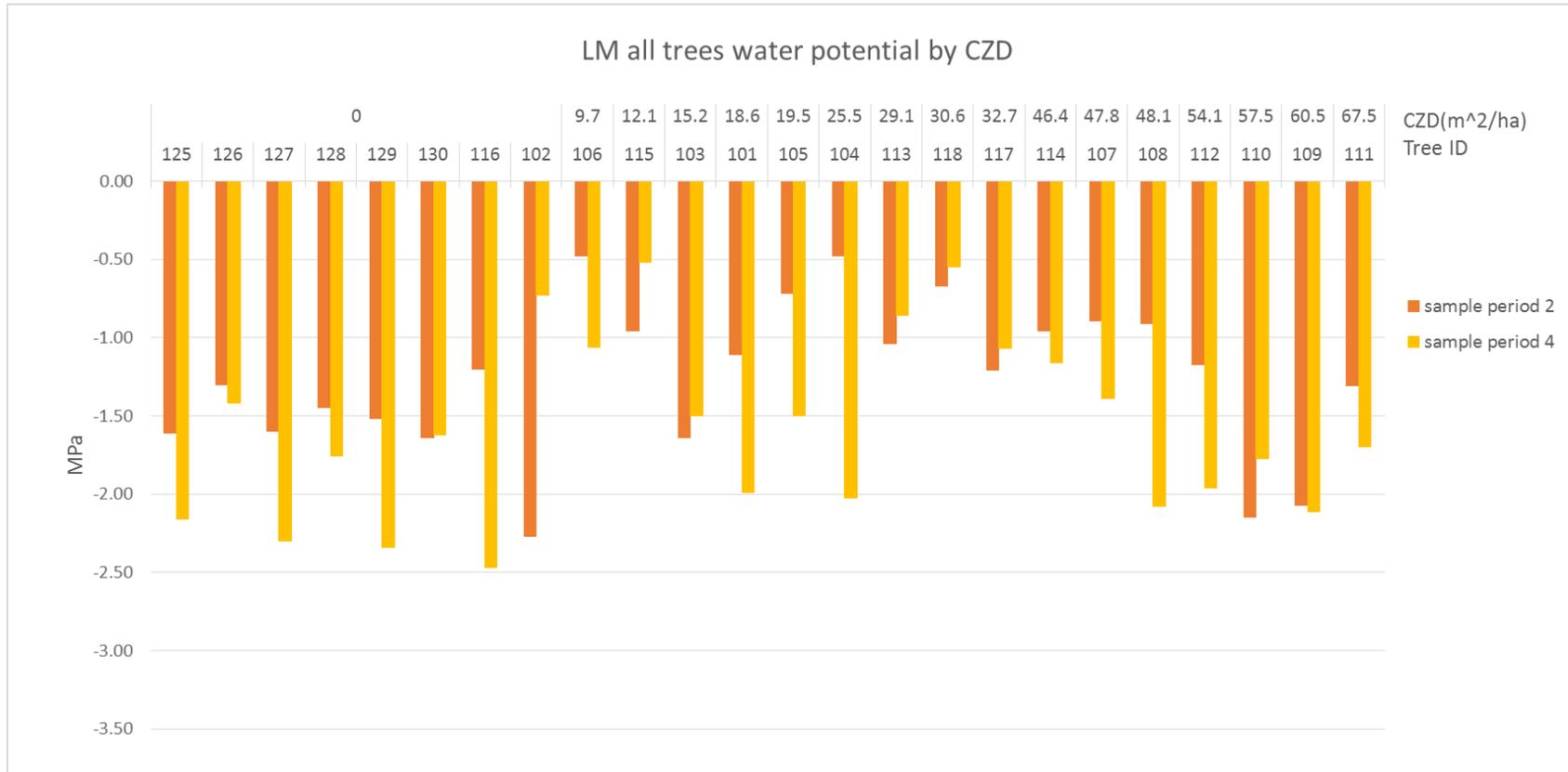


Figure 16. Water potential for all mature ponderosa pine trees sampled at Lookout Mountain (LM) in ascending order by competitive zone density (CZD). Individual trees shown by tree ID tag. Sample period (2 and 4) indicated by color, based on sap flow sample periods. $n=24$ by sample period. Trees LM_119, 120, 121, 122, 123 and 124 were removed from the dataset due to presence of dwarf mistletoe.

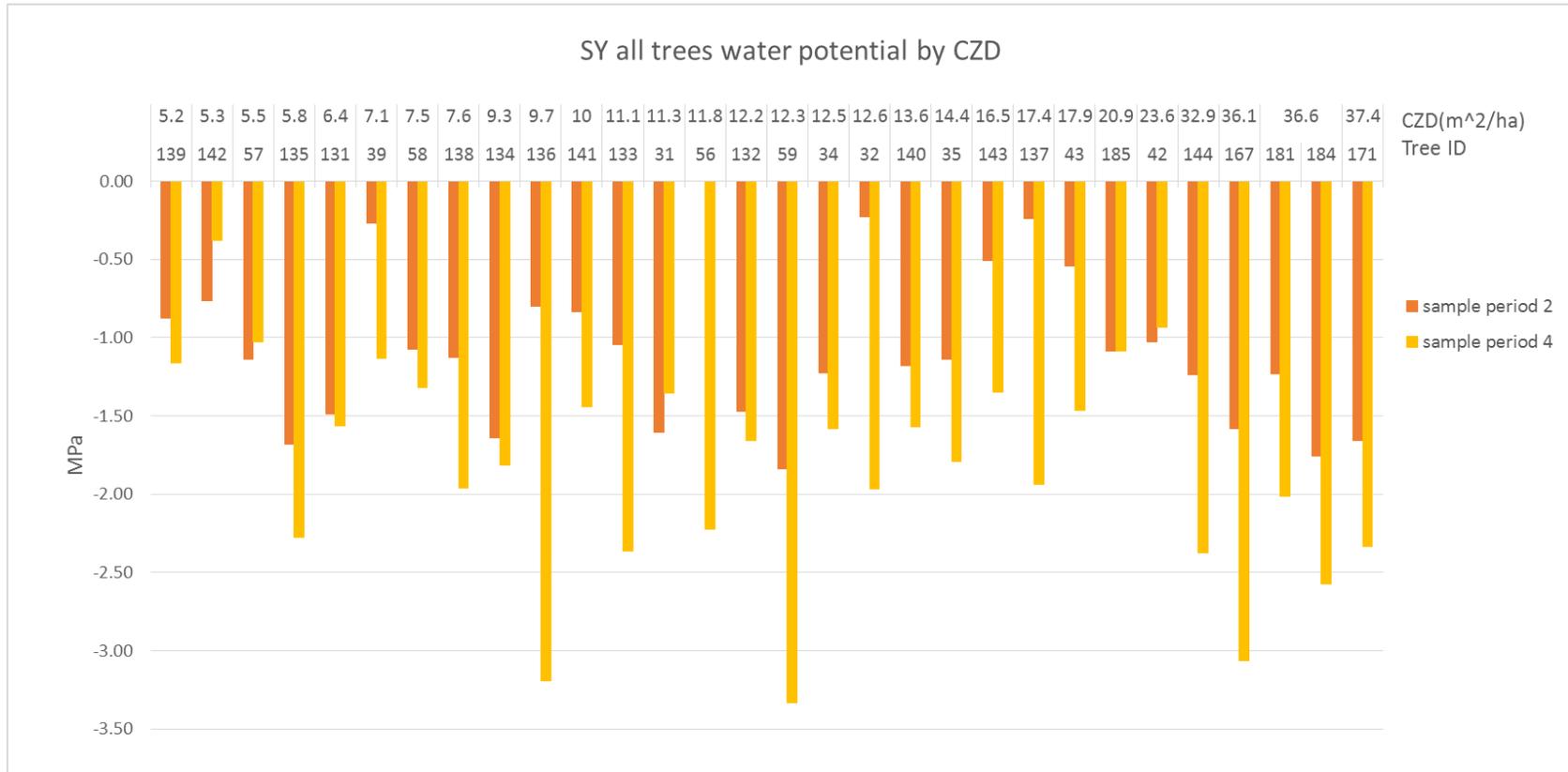


Figure 17. Water potential for all mature ponderosa pine trees sampled at Sycan Marsh (SY) in ascending order by competitive zone density (CZD). Individual trees shown by tree ID tag. Sample period (2 and 4) indicated by color, based on sap flow sample periods. $n=29, 30$ by sample period. Missing value for SY₅₆ (sample period 2) due to faulty psychrometer.

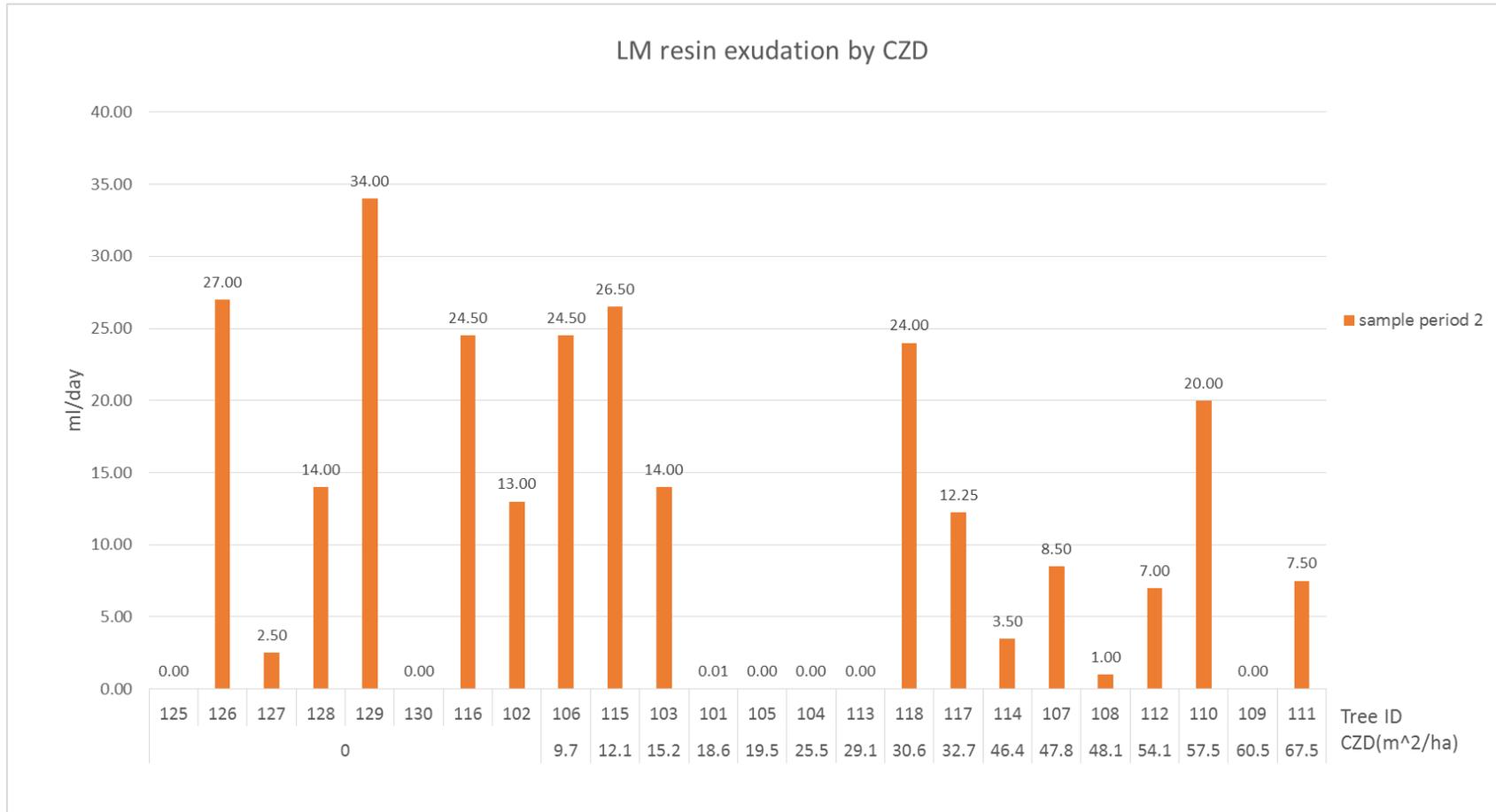


Figure 18. Resin exudation for all mature ponderosa pine trees sampled at Lookout Mountain (LM) in ascending CZD order. Zero values are true results. Sampling date most closely associated with sample period 2 (August 4th 2015). n=24. Trees LM_119, 120, 121, 122, 123 and 124 were removed from the dataset due to presence of dwarf mistletoe.

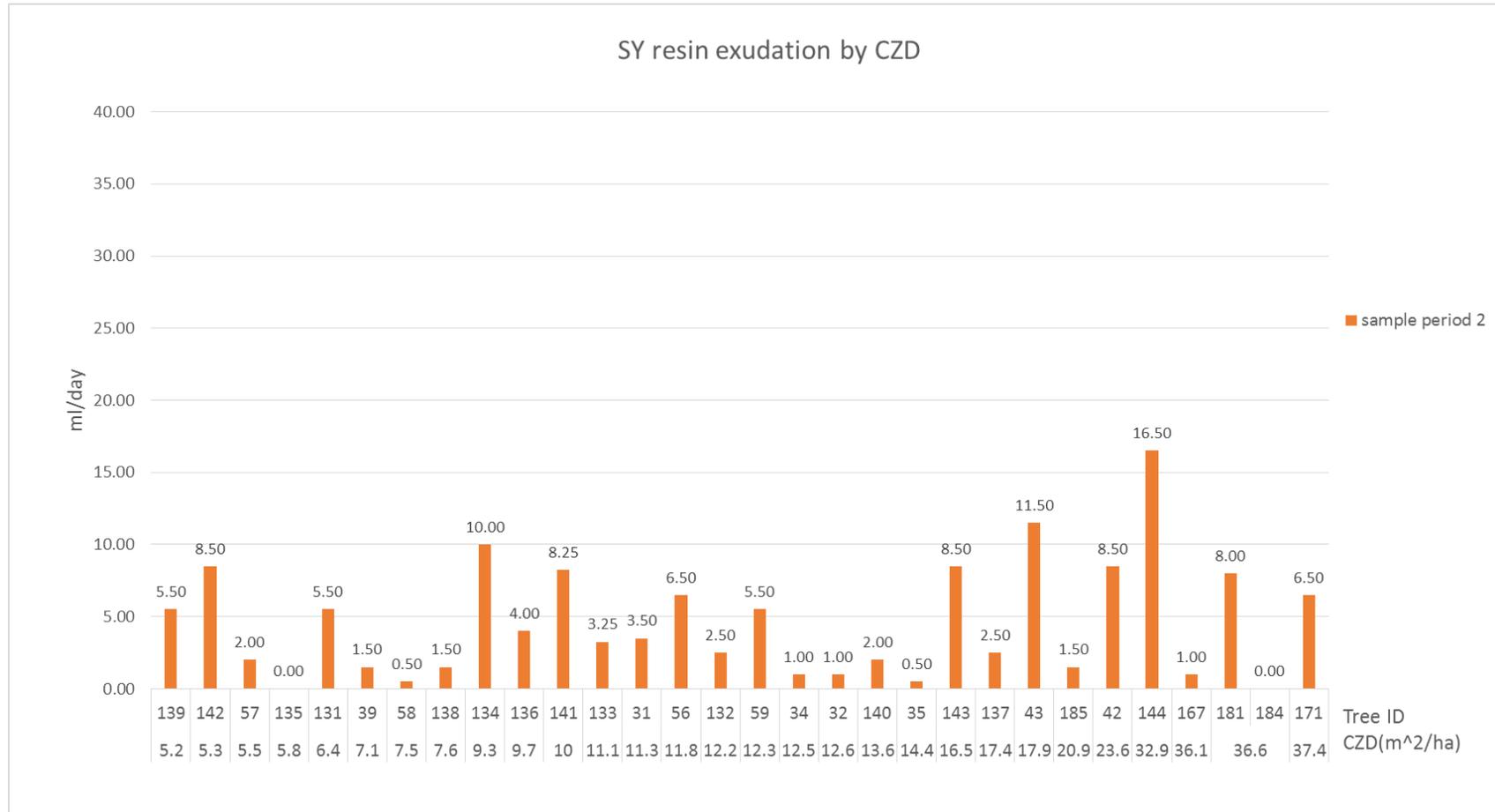


Figure 19. Resin exudation for all mature ponderosa pine trees sampled at Sycan Marsh (SY) in ascending CZD order. Zero values are true results. Sampling date most closely associated with sample period 2 (August 4th 2015). n=30.

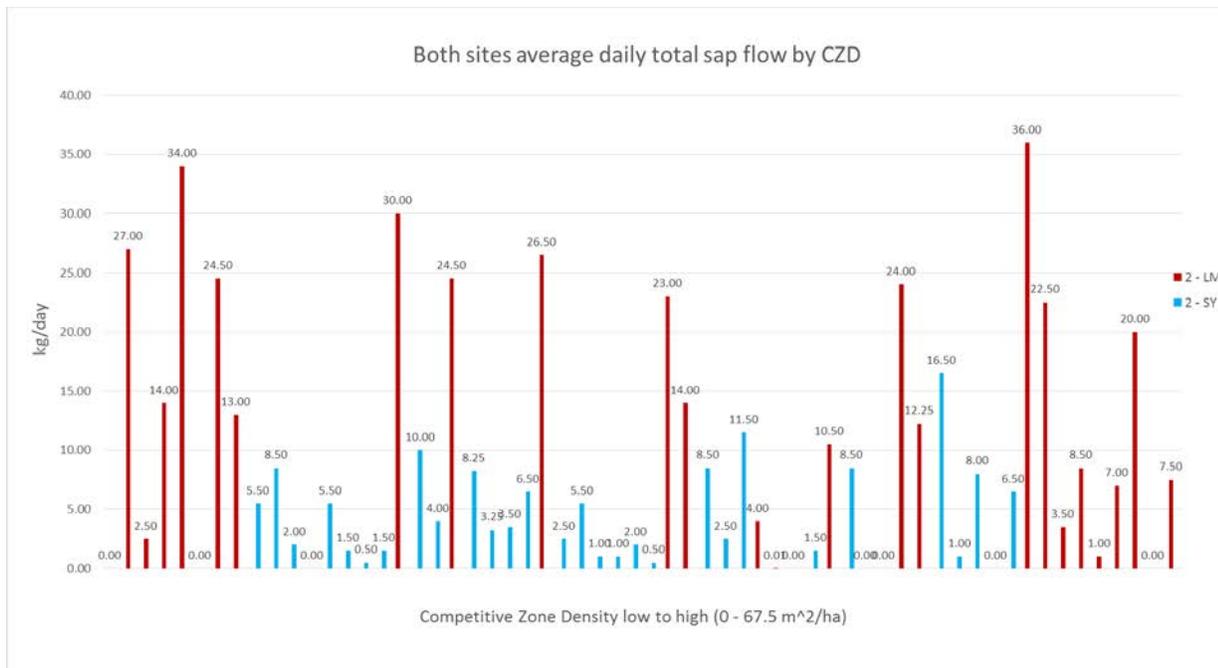


Figure 20. Resin exudation for all mature ponderosa pine trees sampled at Lookout Mountain (LM) and Sycan Marsh (SY) in ascending CZD order. Zero values are true results. Sampling date most closely associated with sample period 2 (August 4th 2015). n=24 (LM), 30 (SY). Red = LM Blue = SY.

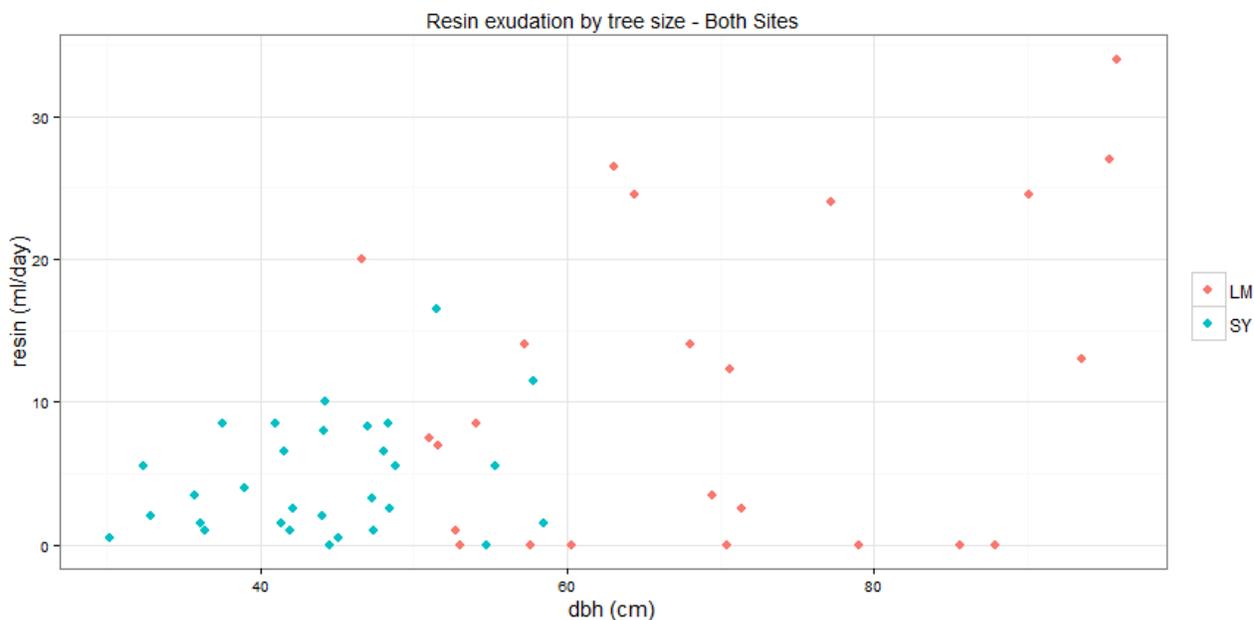


Figure 21. Resin exudation for all mature ponderosa pine trees sampled at Lookout Mountain (LM) and Sycan Marsh (SY) versus tree size in dbh (cm). n=24 (LM), 30 (SY). Red = LM, Blue = SY.

Table 3. Competitive zone density, percent understory cover, neighborhood tree density, average study tree diameter at breast height (dbh) and average tree age for Lookout Mountain (LM) and Sycan Marsh (SY).

Site	Neighborhood	CZD range (m ² /ha)	Understory cover (%)	Neighborhood density (m ² /ha)	Avg dbh (cm)	Avg age (yrs)
LM	01	0-0	64.5	20.32	82.5	153
LM	02	0-46.4	13.67	23.92	76.4	147
LM	03	0-25.5	24.67	29.13	67.2	116
LM	04	8-44.9	23.83	26.01	59.7	112
LM	05	47.8-67.5	45.67	65.03	51.5	109
SY	01	5.8-9.3	63	12.27	47.1	115
SY	02	5.3-16.5	48.33	16.47	41.4	115
SY	03	5.5-17.4	45.67	14.95	39.7	115
SY	04	5.2-23.6	67	16.48	48.2	115
SY	05	20.9-37.4	62.5	43.61	44.2	115

Table 4. Sap flow analysis for Lookout Mountain and Sycan Marsh. t and p-values for explanatory variables, degrees of freedom, estimated slope, 95% confidence intervals, and fit statistics for response of average daily total xylem sap flow (kg/day) from the Lookout Mountain and Sycan Marsh study sites. Competition variables: competitive zone density (CZD, m²/ha), understory percent cover (% under), proportion of trees with greater basal area in CZD (BAL). Quadratic term for competitive zone density (CZD²) included in the model to account for curvilinear relationship observed in the data. Environmental influence variables: soil water content (SWC, m³/m³), and potential evapotranspiration (PET, daily average in mm). Values of p<0.05 shown in bold. Pseudo R² fit statistics are reported for LM and SY models.

	Lookout Mountain sap flow					Sycan Marsh sap flow				
	t	df	p	est. slope	95% CI	t	df	p	est. slope	95% CI
CZD	2.845	20	0.010	34.06	10.27 – 57.85	0.175	25	0.863	2.77	-28.71 – 34.25
CZD²	-2.376	20	0.022	-4.58	-8.42 – -0.75	-0.024	25	0.981	-0.09	-7.27 – 7.10
% under	-1.445	20	0.160	-0.48	-1.15 – 0.18	-0.282	25	0.781	-0.05	-0.42 – 0.32
BAL	-1.493	20	0.151	-61.06	-142.31 – 20.20	-0.734	25	0.470	-10.41	-38.55 – 17.73
SWC	2.839	9	0.019	819.88	245.87 – 1393.90	-0.294	12	0.774	-33.49	-259.17 – 192.20
PET	1.911	9	0.088	11.70	-0.47 – 23.88	1.913	12	0.107	-0.08	-7.27 – 7.10
	PsR²c	0.88				PsR²c	0.81			

Table 5. Water potential analysis for Lookout Mountain and Sycan Marsh. t and p-values of explanatory variables, degrees of freedom, estimated slope, 95% confidence intervals, and fit statistics for response of bole water potential (MPa) from the Lookout Mountain and Sycan Marsh study sites. Competition variables: competitive zone density (CZD, m²/ha), understory percent cover (% under), proportion of trees with greater basal area in CZD (BAL). Environmental influence variables: soil water content (SWC, m³/m³), and potential evapotranspiration (PET, daily average in mm). Values of p<0.05 shown in bold. Pseudo R² fit statistics are reported for LM and SY models.

	Lookout Mountain water potential					Sycan Marsh water potential				
	t	df	p	est. slope	95% CI	t	df	p	est. slope	95% CI
CZD	2.792	20	0.013	0.035	0.09 – 0.61	0.257	25	0.799	0.11	-0.11 – 0.94
CZD²	-2.493	20	0.024	-0.05	-0.09 – -0.01	-0.833	25	0.413	-0.08	-0.28 – 0.12
% under	-1.335	20	0.222	-0.004	-0.01 – 0.002	-0.419	25	0.679	-0.002	-0.01 – 0.008
BAL	0.479	20	0.631	0.21	-0.67 – 1.10	-0.450	25	0.656	-0.15	-0.15 – 0.52
SWC	1.027	3	0.425	4.18	-4.98 – 13.34	0.370	4	0.730	2.56	-11.32 – 16.44
PET	-0.913	3	0.607	-0.10	-0.47 – 0.27	-1.367	4	0.265	-0.19	-0.46 – 0.09
PsR²c	0.35					PsR²c	0.68			

Table 6. Resin exudation analysis for Lookout Mountain and Sycan Marsh. t and p-values of explanatory variables, degrees of freedom, estimated slope, 95% confidence intervals, and fit statistics for response of resin exudation (ml/day) from the Lookout Mountain and Sycan Marsh study sites.. Competition variables: competitive zone density (CZD, m²/ha), understory percent cover (% under), proportion of trees with greater basal area in CZD (BAL). Environmental influence variable: seasonally averaged soil water content (avgSWC, m³/m³). Values of p<0.05 shown in bold. Pseudo R² fit statistics are reported for LM and SY models.

	Lookout Mountain resin exudation					Sycan Marsh resin exudation					
	t	df	p	est. slope	95% CI	t	df	p	est. slope	95% CI	
CZD	-3.364	16	0.002	-8.92	-14.12 – -3.72	2.164	21	0.042	6.02	0.23 – 11.80	
CZD²	1.461	16	0.163	0.60	-0.27 – 1.46	-1.643	21	0.115	-1.18	-2.68 – 0.31	
% under	1.766	16	0.096	0.19	-0.04 – 0.41	-0.439	21	0.665	-0.01	-0.08 – 0.05	
BAL	3.736	16	0.002	27.37	11.84 – 42.90	-2.965	21	0.007	-5.70	-9.70 – -1.70	
avg SWC	-0.632	2	0.592	-104.77	-817.50 – 607.96	1.094	3	0.354	24.77	-47.28 – 96.83	
PsR²c	0.44					PsR²c	0.29				

CHAPTER 6 – DISCUSSION

This study supports assertions that reducing stand density through actions such as thinning and burning is beneficial for tree water use, and shows that these benefits can extend to mature ponderosa pine. At the individual tree level this suggests that management actions can lead to more vigorous mature tree performance, which in turn has implications for overall stand resilience. Mature trees, through increased resistance to fire and drought, can persist through such disturbances, helping to keep the overall forest system intact and provide resources for stand recovery. Study results aligned with the underlying conceptual framework (Figure 1), but not necessarily according to the original hypotheses. The first hypothesis, positing that tree vigor and available resources are connected, was borne out by the simultaneous decreases observed in sap flow as soil moisture declined over the season. Changes in stem water potential were less distinct but over half the total sample showed evidence of a decline in water status from mid- to late-season, suggesting an overall decrease in tree water status as soil moisture declined. The relationship between resin exudation and site resource availability was inconclusive.

Secondly, it was expected that the availability of resources would be positively affected by decreasing competition. The inverse correlation between soil moisture and CZD at LM supported this hypothesis as well, though the same correlation was not found at SY. However, in this study the aim of characterizing the soil moisture condition was not to understand true moisture availability for the study trees. SWC was measured repeatedly from June to October primarily to capture its change over time, and provide context for the corresponding changes in the response variables, if assumptions proved correct. SWC also indicated possible relative differences in water resources among neighborhoods at each site, but these differences cannot be seen as definite. Distribution of water in the soil profile is not uniform across an area; it would have taken more than two sampling sites per neighborhood to estimate actual soil moisture conditions. Most importantly, CZD was assessed at the tree scale, while SWC was assessed at the neighborhood scale. This difference means any correlation between SWC and CZD at LM holds less inferential power than measured changes in SWC over time. It can still be stated that on the whole SWC was observed to be higher and remained elevated longer at SY than at LM, but the water availability experienced by individual trees at each site may not have reflected this general trend.

Other site differences between LM and SY neighborhoods besides SWC may have played a role in the discrepancies in the statistical significance of the fitted relationships. CZD did not range as widely at SY as at

LM, and tree sizes were smaller at SY as well. The ability to perceive potential competitive influences was therefore more limited at the SY site. The intent of sampling at two sites was in fact to see if vigor-density relationships were consistent despite site differences, but to some degree the overall conclusions were inhibited by the fact that SY did not cover the same range of CZD as did LM, and in fact reached its upper limit right at a key threshold point observed at LM. Consistent tree size across the range of CZD at LM would also have strengthened the interpretative potential of the results.

Thirdly, it was hypothesized that if reducing density increases available resources, and that more resources support greater tree vigor, then reducing density should increase tree vigor. This aspect of the conceptual framework proved to be the least straightforward. A linear relationship was expected between tree vigor and tree competition; as competitive zone density increased, vigor indices would correspondingly decrease. As it turned out, the sap flow and water potential to CZD relationship was better characterized by a hyperbola, with sap flow actually increasing as CZD increased up to about 4m²/ha, then dropping off thereafter. This suggests a facilitative effect of CZD among mature ponderosa pine, perhaps due to hydraulic redistribution (Dawson 1993, Domec et al. 2004), shared mycorrhizal networks (Korb et al. 2003, Simard and Durall 2004), or reduction of soil evapotranspiration and temperature due to increased shade (Holmgren et al. 2012, Holmgren et al. 1997). Fichtner et al. (2015) compared the impacts of density above and belowground for old-growth trees, and found that the effects on tree radial growth from belowground competition were less than the effects from canopy shading, and that each impact can mitigate the other, suggesting that density is more nuanced in its effects for older trees. Quadratic relationships between stand-level density and growth indicators were also found in analyses of Oregon and California ponderosa pine stands (Zhang et al. 2013), and in other tree density - growth comparisons (Linares et al. 2010). However, in a separate study with a significantly large sample size (5,032 trees over 14 sites), linear inverse relationships were found between individual tree growth efficiency and tree competition (Woodall et al. 2003). Scaling up of this particular study to a similar size would require extraordinary resources, but the observed relationships for water use, vigor and competition at such a sample size would likely yield some extremely useful insights.

The high degree of variability found in the sap flow and water potential responses may also indicate that at lower densities, water-related responses of mature trees are not as affected by surrounding density as they are by other factors. Tree size, dbh, BAL and understory plant competition were examined visually within the relationship between sap flow and CZD to see if any of these might help explain why trees at similar densities moved sap at such different rates. However, no discernable patterns were found. At a certain threshold,

however, this study showed that the presence of other trees does appear to become a biologically-significant negative influence, ultimately aligning with original expectations.

An examination of how sap flow and water potential related to one another was useful for understanding water resource use more generally in this study. The change in both sap flow and water potential from late-July to late-September (sample periods 2 and 4 respectively) was clearly shown by a graphic representation of their relationship (Figure 22). Sap flow and water potential appeared to be positively correlated with one another, as sap flow values above 100 kg/day concurrently had water potential values of -1.7 MPa or higher, and all water potential values below -2.0 MPa did not reach sap flow values greater than ~55 kg/day. Conversely, both were negatively correlated with time (period 2 to period 4), which in this study was a proxy for soil moisture decline. Therefore, as SWC diminished, a tree's ability to move water and to have water available to do work were both likely to be negatively impacted. Furthermore, the lower an initial water potential or sap flow value, the more likely for a stressed condition to occur later in the season. Trees below a bole water potential of -1.8 MPa did not have average daily sap flows above a rate of ~55 kg/day for the mid-season (sample period 2) or late-season (sample period 4) measurement. (Note that numerous trees with sap flow rates below 55 kg/day had water potentials above -1.8 MPa.) Bole water potential didn't drop below -2.27 MPa for any tree in the first sampling period. However, for trees with sap flows below 55 kg/day at mid-season, water potentials tended to continue to become more negative in late-season, with many of these trees experiencing bole water potentials below -2.0 MPa. As previously stated (see Chapter 2), it can be assumed that even trees with bole water potentials greater than -2.0 MPa bole water potentials were experiencing lower canopy water potentials and the onset of widespread stomatal closure. By this metric, observing sap flow values of less than 55 kg/day could be an indicator of emerging water-related tree stress. These estimates only apply to the trees in this study, but generally suggest that tree water use early in the season has a role in the vulnerability of the tree to stress later on. Lastly, study trees with CZDs over 35 m²/ha were more likely to have sap flow rates at the beginning of the season that were below the 55 kg/day mark, suggesting that increased competition at the onset of the growing season creates increased vulnerability to water stress later in the season. Vulnerability increases in part as a consequence of lower photosynthetic production, which reduces the tree's ability for effective growth and maintenance or to build its capacity to access needed resources (Richardson 1998).

More encouragingly for mature pine, this also suggests that more effective resource access early on can buffer a tree against stress as conditions become more difficult. Domec et al. (2004) found that with hydraulic redistribution, soil water potentials in 280 year-old ponderosa pine stayed above -2.0 MPa through the dry

season, compared to a young ponderosa pine stand lacking hydraulic redistribution (due to less deeply developed root systems), where soil water potential decreased to -2.8 MPa. This severely impaired the root functioning in the younger stand and slowed recovery when drought conditions were alleviated. The older trees proved more resilient to the same drought conditions, maintaining much higher stomatal conductance by a delayed loss of root conductivity. This advantage of mature pine physiology may be enhanced by a moderate amount of neighboring trees, and furthermore may help support a wider diversity of plant species and consequently other organisms.

The same kinds of relationships were not visually apparent for resin exudation with either sap flow or water potential, however. Low (or zero) to high amounts of produced resin could be observed across the range of either response variable. It's likely that resin exudation is more strongly influenced by other factors in the tree or environment than water access. Likewise, exploration of the CZD ~ tree vigor relationship via resin exudation was less conclusive. Resin exudation did not show a statistically significant relationship to CZD at either site; and as the nature of the relationships were quite different for each study site, correlations are not readily inferred. Why low to moderate CZDs would correspond with increasing resin production at SY and then with decreasing resin production at higher densities is hard to ascertain. LM's negatively asymptotic trendline is more in line with the ideas of resource stress affecting carbon allocation priorities away from self-defense. It also fits with studies that show resin flow and water stress in ponderosa pine to be inversely related (Lorio et al. 1990). However, the fact that there were trees that produced no resin along the entire CZD continuum is difficult to account for. Little evidence of beetle activity was observed in 2015 at LM, and while previous beetle activity was noted at SY in general, trees selected for study were free of pitch tubes or other visual indicators. Other forms of infestation, infection or damage noted were either accounted for (removal of all trees at LM 04 from analysis due to dwarf mistletoe) or appeared unrelated to the pattern in resin exudation. Interestingly, all six trees removed from the study due to dwarf mistletoe exuded some amount of resin (none were zero-producers, or even near-zero). Furthermore, trees in a given neighborhood displayed a wide range of resin production, reducing the likelihood of a microclimatic rationale for resin exudation amount. Neither were there clear relationships between resin exudation and sap flow, or between resin and water potential.

Other studies have shown resin duct formation to have a positive connection with radial xylem growth in ponderosa pine (Kane and Kolb 2010), which may help to explain the greater resin volumes produced in the larger LM trees in this study. As radial tree growth is positively linked to resource availability (Wallin et al. 2004), a relationship of this vigor measure to competition would then certainly exist as well. That said, there is

a great deal of inconsistency in the literature regarding resin duct formation and diameter growth. Kane and Kolb noted a high degree of variability in resin duct formation among trees despite being in the same place and of comparable size, which was also found in this study. However, the authors suggested that genetics would also have a strong influence in regulating carbon allocation for self-defense, so that the link between resource use, growth and resin duct production might be mediated by individual genetic predisposition. Recent work looking at resin and disturbances such as fire has shown that low-severity fire stimulates the formation of resin ducts in ponderosa pine, and conversely that a lack of regular low-severity fire lessens this tendency over time (Hood et al. 2015). Results of other research support this finding (Davis et al. 2011, Zausen et al. 2005, Wallin et al. 2004). This suggests that resin production may be more pulsed than continual, and less linked to resource availability than to regular disturbance, which is also supported by other studies (Gaylord et al. 2011). Prescribed fire was implemented at both sites in this study, but treatment at LM occurred in 2014 as opposed to in 2013 at SY. Therefore it is possible that the overall higher exudation rates at LM were linked to experiencing fire more recently, though this supposition is undermined by the numerous trees that produced no resin across the LM neighborhoods. Overall, the results of this resin exudation investigation would imply that the connection between self-defense and CZD for mature ponderosa pine exists, but is one piece of a complicated network of factors, ones that may cause the defense-competition relationship to be positive or negative.

Finally, comparing the results of the study at each site provides some insights for this and future studies. Across all response variables, LM exhibited a more 'vigorous' response, with higher rates of sap flow, less negative water potentials, and greater production of resin. Moreover, these responses were produced in an environment with possibly less available soil moisture and similar atmospheric demand, though actual water access by the trees in this study can only be inferred from the sap flow and water potential data, which indicate that LM was more successful in this respect. Why were the study trees performing better at LM than at SY? It's quite possible this was a consequence of size, the most obvious difference between the sites. Larger trees have been found to rely on water from deeper in the soil profile (Kerhoulas et al. 2003), and make it more accessible at higher levels by bringing it closer to the soil surface (Caldwell and Richards 1989). Age was another key difference, as LM trees were about 30 years older on average than SY trees. In other studies, mature ponderosa pine have been shown to have greater water use efficiency than younger pines (Irvine et al. 2004). Older trees may have a greater tolerance for competition due to a proportionally lower need for water, combined with a greater below and aboveground infrastructure for accessing it (Richardson 1998, Martinez-Vilalta et al. 2004). Of course, unaccounted-for factors may have played a role, including available nutrients, genetics, or damage/disease not noticed during sampling. The contrasts in understory

plant composition between the sites also point to other factors at play. The presence of greenleaf manzanita, ceonothus and prince's pine at LM is associated with greater site productivity characteristics in ponderosa pine forests, in contrast with SY's predominantly grass and forb assemblage (Volland 1985, Emmingham et al. 2005). If size and age were key factors, however, this further underscores the importance of retaining older, bigger trees to enhance drought resistance in dry forest landscapes.

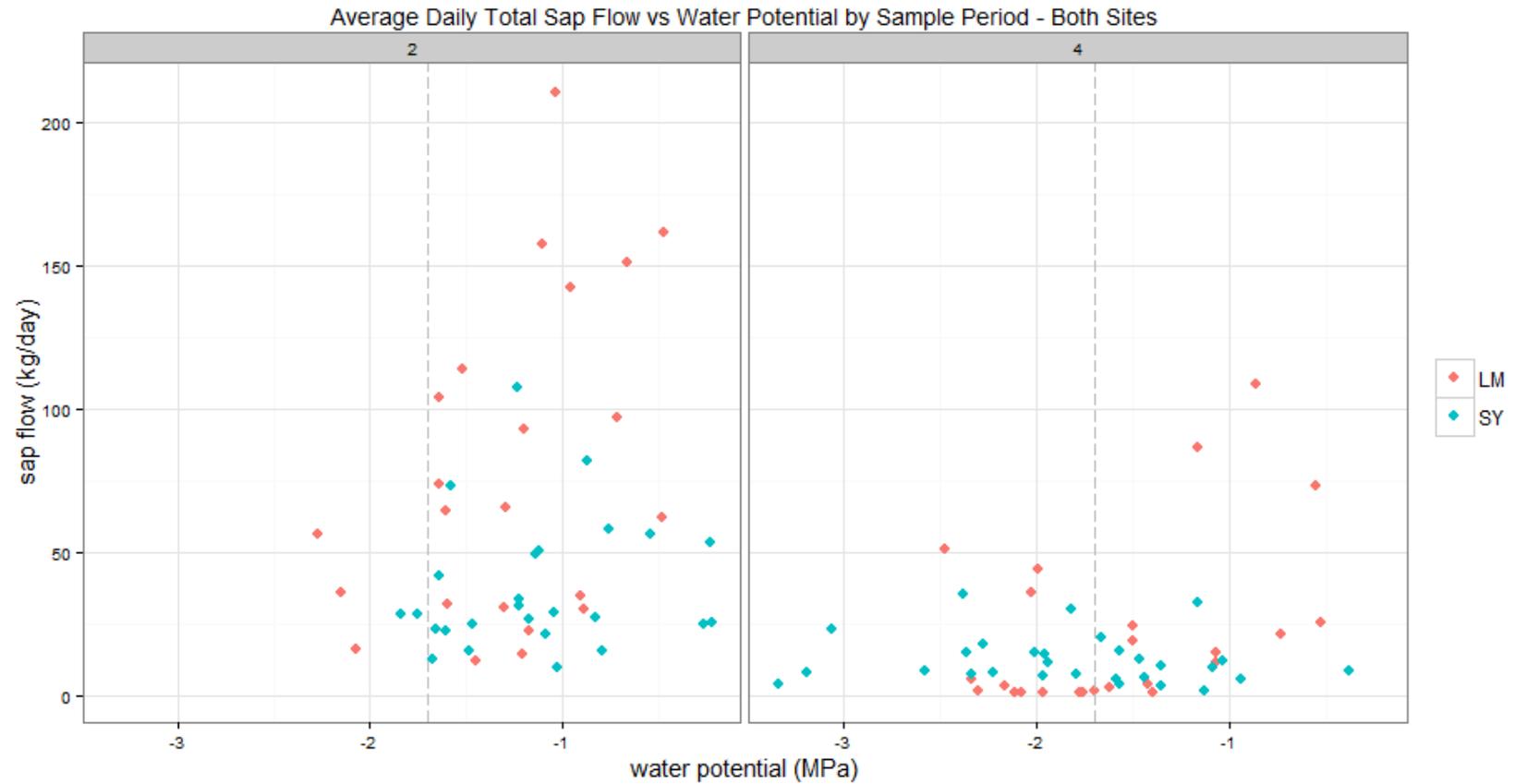


Figure 22. Average daily total sap flow and water potential relationships for all sampled mature ponderosa pines at Lookout Mountain (LM) and Sycan Marsh (SY) by sample period. Dotted grey line indicates the threshold of initial stomatal closure in ponderosa pine (-1.7 MPa). Sampling period notation (2,4) based on sap flow sample periods. n=24 (LM). 30 (SY) by sample period. Red = LM, Blue = SY.

CHAPTER 7 - CONCLUSIONS

This study, in seeking to contribute to our understandings of how to support mature ponderosa pine in the dry forest landscape, focused on performance, not simply growth. Forest structural and compositional changes as a result of human influence have already impacted the vigor and resilience of ponderosa pine stands in the intermountain west. Widespread forest loss in many parts of world is occurring as a result of increased susceptibility to drought and secondary stressors. Understanding the connections between tree density and key life-supporting behaviors such as water use and self-defense for mature ponderosa pine is therefore of high value, as mature trees are the most difficult to regain in a forest once they are gone. Future study across more trees over a wider range of sites, moisture conditions, and post-treatment densities would further hone in on both the mean and range of the physiological response of mature ponderosa pine across the spectrum of surrounding competition. This would help clarify the actual extent of the influence of competitive density on mature ponderosa pine, as well as more precisely define where threshold responses to competition may exist for these trees. Additionally, comparing changes in physiological response before and at several intervals after reductions in tree competition would be of use for better understanding the duration of physiological benefit from management action for mature ponderosa pines. Lastly, tracking tree response over multiple seasons would also improve our understanding of their response to variations in climate.

In forest ecosystems, tree density at individual scales is going to vary by tree, especially if management goals are to promote ecologically beneficial outcomes. Spatial heterogeneity in forests has been championed for increasing ecosystem resilience to disturbances, supporting a range of wildlife uses, and fostering different successional stages in the landscape. Making major reductions in ponderosa pine stand density has been emphasized to increase tree productivity and reduce vulnerability to fire, pests, and drought. Thinning and burning can be employed to foster variability even as these treatments boost tree and stand resilience. At the same time, the retention of larger, older tree specimens is desired - and mandated for many lands. There may be nuances to the benefits of thinning and burning for mature trees, however, which merit consideration in forest management practice. Stand density targets, for example, might incorporate an appreciation of possible facilitative benefits of tree density. Overly-heavy thinning of Oregon's mature ponderosa pine stands may reduce the benefits of proximity to neighboring trees which aid in water resource access. Mature ponderosa pine may exhibit a variety of physiological responses, including positive ones, as surrounding tree density increases. On the other hand, there appears to be a threshold at which competition outweighs facilitation and instead increases drought-stress vulnerability. Overall, a drive for increased spatial and structural

heterogeneity in forest systems can be conducive to a range of management aims - as long as we continue to support mature trees, which are at once critically beneficial and essentially irreplaceable.

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