Quaking aspen, *Populus tremuloides*, has experienced severe declines in recent years in part due to the effects of changing climate and extreme drought. As the dominant deciduous tree in Western North American forests, aspen plays a critical role in forest biodiversity and ecosystem function. Therefore, the persistence of this species under changing climate patterns is a topic of critical concern; especially where aspen exists toward the vulnerable margin of its range. This study set out to investigate the associations of atmospheric, hydrologic, edaphic and topographic variables with physiological drought stress in aspen. The study took place on the Zumwalt Prairie in northeastern Oregon, a semi-arid bunchgrass prairie where aspen occur in isolated stands associated with riparian areas and late-season persistence of snow drifts. Using a 33-year time series of landsat imagery to detect associations of aspen stands late-season snow cover and field measurements of soil moisture in aspen stands during 2017, we found while snow dominated stands were associated with greater soil moisture during spring, levels had equilibrated to those of other upland stands by summer. Measurements of predawn and midday
stem water potential in multiple height classes of aspen ramets revealed associations of both shallow soil moisture and vapor pressure deficit with physiological drought stress in aspen. Analysis of soil texture class revealed an important association with midday stem water potential, with finer textured soils associated with somewhat higher midday drought stress than coarser textured soils. While neither topographical characteristics nor snow cover were found to be important drivers of drought stress, topographical curvature was found to have a strong influence on summer soil moisture in upland stands. These findings contribute to our understanding of aspen physiology, drought ecology and landscape hydrology toward the xeric margin of aspen’s range. This information can help land managers to anticipate and adapt to changing climates and understand their effects on key plant species such as aspen.
Aspen Drought Stress Response, Snow Cover, and Soil Moisture Dynamics on an Oregon Bunchgrass Prairie

by

Andrew Neary

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APPROVED:

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Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Andrew Neary, Author
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CHAPTER 1 – INTRODUCTION

Background on *Populus tremuloides* Michx.: Ecology, disturbance and drought-induced mortality

*Introduction*

Quaking aspen, *Populus tremuloides* Michx., is a short-lived, deciduous tree species that forms extensive clonal colonies. Aspen is commonly found growing 6 to 18m tall and 8 to 46 cm in diameter with smooth, white bark, and cordate leaves 4 to 8 cm in diameter. Leaf petioles are flattened perpendicular to the blade, resulting in leaf fluttering when exposed to a breeze. Aspen is an important species in arid landscapes of the Western US where it provides key ecological services and functions (Jones and Debyale 1985).

*Ecological and Economic Importance of Aspen*

Quaking aspen is an ecologically important tree species, especially in the Western US where it is one of the only widespread deciduous tree species in montane habitats. In the Western US, aspen occupies a diversity of habitat types where it contributes substantially to ecological function and biodiversity. Aspen stands and their associated understory vegetation are considered a distinct forest type in the intermountain west, where they host unique assemblages of species compared to other habitats. In comparison to meadows and conifer forests, aspen forests have been found to host more overall plant species and higher numbers of unique species.
(Kuhn 2011). In comparison to conifer forests, aspen stands have significantly higher snow water
equivalent, likely due to their deciduous nature (LaMalfa and Ryle 2008, Burke and Kasahara
2011). The production of prolific leaf litter is also likely responsible for driving important
nutrient cycling functions within aspen stands which have been found to exhibit increased levels
of soil respiration, N, K and soil organic matter compared to conifer stands (Buck and St. Claire
2012). Additionally, while soil organic carbon (SOC) concentration is not significantly higher in
aspen stands, it is considered to be stored in a more stable form in comparison to conifer stands,
potentially buffering forest SOC stocks against global change (Laganière et al. 2017).

Aspen stands also provide key ecological structure and function in support of avian
communities. Aspen’s susceptibility to heart rot makes it an important species for cavity nesting
birds and bats (Dobkin et al. 1996, Swift et al 2017). Compared to nearby ponderosa pine
stands, aspen stands have been found to host a higher richness and diversity of bird species
(Griffis-Kyle 2003, Sallabanks et al. 2005, Swift et al. 2017). Furthermore, it has been suggested
that avian diversity may benefit from greater insect richness and abundance in aspen stands
(Sheperd et al. 2006) and aspen stands have been shown to host different insect community
composition than nearby grasslands (Gonzalez et al. 2011).

Aspen stands also serve key ecological functions for many mammal species including
beaver, elk, deer and domestic livestock. Beaver use aspen extensively as both a material for
dam and lodge building as well as a food source (Mcolley et al. 2011). Elk and deer consume
young aspen as a highly nutritious, preferred browse species especially during fall and winter
when other forage may be limited or of poorer quality (Jones and Debyle 1985, p117). As areas
of high forage production and quality, aspen stands also attract cattle and sheep who consume
young aspen and seek shade within the tree canopy during summer months (Debyle and Winokur 1985, p117).

In addition to aspen’s ecological importance, it is considered a culturally important tree species for its economic, aesthetic, recreational and medicinal values. Aspen is an important commercial timber species in some regions of Canada and the Great Lake States especially for pulp, composite products and other specialty products. As a wood product, aspen is soft, light and does not splinter, making it particularly suitable for boxes, paneling, flooring, toys and matchsticks (Petersen & Petersen 1992). Aspen is highly regarded for its aesthetic value especially in western landscapes where its bright, green foliage contributes a distinct textural contrast to conifer forests, shrublands and grasslands. Aspen’s aesthetic appeal is especially attractive during autumn months when its changing leaves produce brilliant displays of color in otherwise evergreen dominated western landscapes. In part for these reasons, aspen stands are valued for recreational opportunities and many are host to campgrounds and scenic hiking, biking and horseback riding trails. In addition to these contemporary cultural values, historically native peoples used aspen cambium and catkins as a food source, and preparations of the bark as a medicine to treat numerous ailments (Willard & McCormick 1992).

Aspen Genetics

Quaking aspen is a highly diverse plant species both genetically and ecologically. At one time or another, this diversity has led to quaking aspen being subdivided taxonomically into several distinct species and forms, yet more recently it has become widely accepted as a single species (Debyle & Winokur 1985, p 7). Much of this taxonomic challenge has been due to the high phenotypic variability in aspen on both local and regional scales as an expression of genetic
and habitat diversity. Aspen is regarded as one of the most genetically diverse tree species (Kanaga et al. 2008). This is especially true in portions of aspen’s range where sexual reproduction is common, such as the boreal forests of Canada and the eastern US (Callahan et al. 2013). In the western US, sexual reproduction via seed is less common and clonal reproduction often dominates. Genetic diversity of aspen ramets in these landscapes is generally lower (Callahan et al. 2013), yet the diversity of habitat types occupied by aspen is high. In the Western US, aspen stands occupy habitats ranging from isolated, snow-pocket concavities, riparian bottomlands, shrublands, grasslands and mixed conifer forests, among others. In much of its western range, suitable aspen habitat is mediated by topographical characteristics that may influence the temperature and moisture envelop in which aspen can persist. Generally, aspen requires relatively moist sites of between 41 to 102+ cm of moisture where winters are cold (Debyle and Winokur 1985, p 10), yet this distribution may be further limited by annual temperature (Worrall et al. 2013). Depending on where aspen is found within its distribution, the topographical characteristics of suitable habitat are variable. In the western US, aspen is found growing from sea level to as high as 3,700 m, generally confined to these higher elevations toward the southern end of its range (Debyle and Winokur 1985, p 10). Within this variation, aspen often prefers warmer southern slopes toward the northern end of its range and at higher elevations and east to north slopes to the southern end of its range and at lower elevations (Debyle and Winokur 1985, p 10, Mitton and Grant 1996). While cool temperatures and a short growing may limit the distribution of aspen at northern elevations and higher latitudes (Landhäusser et al 2010), high summer temperatures and drought stress may limit its distribution at lower latitudes and elevations (Worral et al. 2013).
Aspen clones can exhibit a high degree of morphological and physiological variation from one clone to another likely due to the interactions of habitat characteristics and heritable genetic diversity (Kanaga et al. 2008). Morphological variations have been found to change across latitudinal clines (Barnes 1975) and moisture gradients (Kanaga et al. 2008). These interactions can also determine sex ratios of aspen clones with the relative proportion of females to males increasing with decreasing elevations (Mitton and Grant 1996). Independent of topographical characteristics, clone sex can determine other traits, with female clones generally exhibiting higher growth rates, larger clone sizes, higher number of ramets and larger basal area than male clones (Mitton and Grant 1996). In addition to clone sex, the ploidy level of an aspen clone can also have a strong influence on morphological and physiological characteristics. Triploid aspen have been found to exhibit lower stand densities, greater leaf area, leaf mass and stomatal size in comparison to diploid aspen (Greer et al. 2017). While aspen has been found to be predominantly diploid in the majority of its northern and eastern distribution, triploid aspen clones have been found to be common toward the southwestern portion of aspen's distribution (Mock et al. 2012). Consistent with the distribution of triploid aspen in this warmer and drier region, triploid aspen have been found to be more drought adapted with higher water use efficiency, yet simultaneously more vulnerable to acute heat and drought events due to less conservative stomatal control (Greer et al. 2017).

Aspen Demography and Disturbance

In the western US, aspen is primarily found growing in clonal stands that reproduce asexually. In these clonal stands, what appear to be individual trees are in fact genetically identical “ramets” interconnected to one another in sometimes extensive root systems. These
clonal root systems allow aspen to quickly regenerate after periodic disturbance events, such as fires, windthrow, flooding, timber harvest, and fungal or insect outbreaks. These events can remove all or portions of the mature canopy, thereby releasing hormonal control and stimulating vegetative reproduction of clonal suckers from the root system (Shepperd et al. 2006). This method of reproduction appears to be more reliable in drought prone areas where establishment of aspen through seed is unlikely due to demanding germination requirements (Wolken et al. 2010). Aspen clones in these habitats are largely dependent on frequent disturbance events to initiate regeneration and maintain the clone vitality (Swanson et al. 2010). In highly productive stands, ramet density can exceed 500,000 individuals per acre following disturbance (Shepperd 1993). These pulses of regeneration help aspen to outcompete other plant species during initial establishment. By reproducing vegetatively shortly after disturbance, aspen has an early advantage over conifer species which rely on reproduction via seed. Over time, however aspen ramet density is reduced as the stand experiences self-thinning (Shepperd 1993). As density is reduced and resources are made available to other plants, aspen stands may actually facilitate the establishment of conifer species in the understory (St. Claire et al. 2013). Over time, many conifer species become superior competitors for soil resources, space and light, eventually inhibiting ramet growth and overtopping the shade intolerant aspen (St. Claire et al., 2013). For this reason, periodic disturbances such as fire, are an especially important component required to sustain these conifer associated “seral” aspen stands (Kurzel et al. 2007).

Seral aspen stands are commonly characterized by uniform age structures resulting from stand replacing disturbances (Rogers et al. 2013). Following these disturbances, the pulse of even-aged ramets eventually recruits into the overstory and suppresses further aspen regeneration
through hormonal control and shading (Shepperd et al. 2006). In addition to acute disturbance
events, these episodic pulses of regeneration may be driven by favorable climatic conditions or
stand senescence (Kaye 2011; Kurzel et al. 2007). So-called “stable” aspen stands are also found
and are characterized by uneven age structures facilitated by continuous levels of regeneration
beneath the canopy. These stable stands persist through low levels of disturbance and the
development of canopy gaps which allow for regeneration and recruitment of young ramets
(Rogers et al. 2013).

Fire has widely been recognized one of the dominant forms of disturbance promoting
aspen persistence on the landscape (Jones & Debyle 1985, Shinneman et al 2013). This is
epecially true in fire adapted seral aspen stands which may become decadent over time in the
absence of fire (Rogers et al. 2013). Fire can promote asexual reproduction of aspen by
removing mature canopy and other competing vegetation, warming soils, and stimulating lateral
roots into suckering (Jones & Debyle 1985). Intense fire can also clear landscapes to bare
mineral soil resulting in sexual reproduction of aspen from seed given the right climatic
conditions (Turner et al. 2013). Prescribed fire has been used as a tool to manage aspen stand
health especially in conifer encroached stands (Kilpatrick et al. 2003). However, fire should be
used with caution as it has the potential to further damage weakened stands. Most aspen
suckering occurs from shallow parent roots, in one study, 92% of suckers were found to initiate
from roots within 12cm of the soils surface (Schier & Campbell 1978). Intense fire may destroy
these shallow parent roots thereby inhibiting asexual regeneration (Wang 2003). These effects
would likely be amplified in shallow, rocky soils where lateral roots will be confined to more
shallow depths in the soil profile.
Fire can also reduce the resilience of already stressed stands where carbohydrate reserves are inadequate to initiate vigorous post fire sprouting. Asexual regeneration depends on energy reserves supplied by parent roots in order to both initiate development of root buds into suckers, and for suckers to successfully push through the soil surface and begin photosynthesizing (Schier & Zasada 1973). Stands with low root carbohydrate reserves have been shown to have poor reproduction following disturbance in comparison to stands with high root reserves (Landhäusser & Liefers 2002). Fire applied in fall as opposed to spring can help to ameliorate these effects for healthy stands whose reserves fluctuate seasonally, however some chronically stressed stands may still not respond well to treatment (Swanson 2010). Furthermore, repeated disturbance after fire, such as repeated burning or heavy ungulate herbivory, may continue to exhaust carbohydrate reserves and diminish suckering response (Schier et al. 1985).

Stand regeneration and resilience in aspen habitats can also be compromised by high levels of herbivory following disturbance. As a defense against herbivory, aspen can produce high levels of tannins and phenolic glycosides in leaf tissue. High levels of phenoloic glycosides in particular can shift feeding patterns away from aspen, thereby deterring herbivory by insects and ungulates under low to moderate levels of herbivore pressure (Lindroth & St. Clair 2013). These compounds have been shown to increase in new growth following browsing; given that they have been shown to exact a cost to aspen in terms of reduced growth, this feedback may further limit regeneration in stressed stands (Lindroth and St. Clair 2013). At high herbivore concentration these compounds are of little consequence and herbivory may act to limit understory regeneration and contribute to declining stand health (Rogers and Mittank 2014). By browsing young suckers in regenerating stands, high numbers of ungulates can arrest the
recruitment of aspen ramets into the overstory. In stands with an already mature canopy, this can lead to “missing age classes” and a bimodal age distribution of mostly young and mature trees over time (Beschta & Ripple 2010). Following a canopy replacing disturbance event, high levels of sustained herbivory may arrest ramet growth below the browse level and lead to an alternative stable state characterized by predominately short ramets (Beschta et al. 2016).

**Aspen and Drought Induced Decline**

Due to the moisture-driven limitations on aspen distribution (Shepperd et al. 2006; Anderegg et al. 2013) and predictions of climate change, acute drought is receiving specific attention as a major disturbance factor contributing to aspen decline (Hogg et al. 2008; Michaelian et al. 2011; Rehfeldt et al. 2009; Worrall et al. 2008, 2013). A drought during the early 2000’s, accompanied by high levels of heat stress, has been linked to large-scale loss of mature aspen canopy across portions of the Rocky Mountains, the Great Lakes region and the boreal forests of Western Canada (Worrall et al. 2010, 2013; Michaelian et al 2011). Various hypotheses have been put forward regarding the mechanisms responsible for these drought-induced decline events; these include damage by secondary agents, limits to carbohydrate production in root systems, and acute physiological damage to vascular tissue and subsequent loss of conductivity.

The direct physiological consequences of both acute and cumulative drought and heat stress on plants informs understanding of drought-induced aspen decline. Two primary hypotheses have been proposed to explain drought-induced plant mortality; the carbon starvation hypothesis and the hydraulic failure hypothesis. (McDowell et al. 2008). The carbon starvation hypothesis proposes that plant species experience steady declines in nonstructural carbohydrates
due to long term decreases in photosynthetic production. This can lead to impaired metabolic function, decreased biotic defense and reduced ability to perform adequate osmoregulation and maintain turgor (McDowell et al. 2013). The hydraulic failure hypothesis proposes that low soil water status and high evapotranspiration results in highly negative xylem tensions leading to cavitation of xylem vessels by air embolism (McDowell et al. 2008). As air enters the xylem, hydraulic conductivity is lost eventually leading to desiccation of tissue and subsequent mortality. Both of these processes have been examined in aspen, with hydraulic failure presenting compelling evidence for drought-induced decline.

The interactions of drought, stomatal regulation and decreased photosynthesis could potentially create negative feedback loops that reduce aspen growth and the resilience of aspen stands to subsequent drought. As heat and water stress increase transpiration, some plant species respond by closing stomata, thereby avoiding drought stress (Lambers et al. 2008). Aspen in particular, are known to impose a high degree of stomatal regulation during drought to avoid water loss and maintain a high enough leaf water potential to avoid xylem cavitation (Hogg et al. 2000). While this may effectively prevent mortality, it also limits photosynthetic production and consequently impairs growth. At extreme levels of drought stress aspen will also experience defoliation which may further reduce water loss and possibly prevent runaway embolism by reducing transpirational area (Lu et al. 2010). This has been observed in seedlings at 50% loss of stem hydraulic conductivity (Lu et al. 2010) and mature aspen trees under drought stress in the form of earlier fall leaf shed compared to non-drought stressed trees (Anderegg 2012). These physiological effects, however, have not been shown to translate into a reduced production of non-structural carbohydrates as hypothesized by the carbon starvation hypothesis. In fact, aspen
tissue has been found to show increased concentration of non-structural carbohydrates during drought, possibly due to increased osmoregulation required to maintain turgor (Anderegg 2012; Galvez et al. 2011). Given that these increases in nonstructural carbohydrates occur alongside reductions in growth, this indicates a tradeoff whereby aspen sacrifices growth in favor of drought tolerance.

During drought conditions, aspen may also experience severe declines in fine root growth and root biomass (Anderegg 2012; Worrall et al. 2010). The consequence of these declines may be dramatic as aspen root systems are critical in vegetative reproduction and hormonal regulation and may be important in sharing of carbohydrates among the clone (Lieffers et al. 2001). Over time, these accumulated losses in roots could negatively affect the ability of aspen to uptake water and nutrients and may render aspen clones more susceptible to successive droughts or other disturbances by limiting their reproductive capability (Anderegg 2012). While aspen mortality has not been directly linked to reduced photosynthetic production or carbohydrate reserve limitation, the accumulated consequences of drought on aspen growth and resilience may be severe (Anderegg 2012, Hogg 2005). In fact, Colorado forests experiencing aspen dieback following drought have been found to exhibit weak regeneration for several years following drought and heat stress (Worrall et al. 2010, 2015).

Recent evidence has been mounting regarding the role of hydraulic failure in drought-induced tree mortality (Hartman et al. 2015). Hydraulic failure occurs when xylem embolism leads to severe restriction of water transport and subsequent desiccation of tissue. Hydraulic failure can lead to reduced growth and, if severe enough, mortality of the plant (Mcdowell et al. 2013). Embolism enters the xylem during high levels of water stress by way of cavitation. This
occurs when xylem tensions are negative enough to cause air to enter the vessel through pores in the vessel (Sperry et al. 1988). The relative vulnerability of a plant to cavitation is dependent on the permeability of these membranes (Lambers et al. 2008). Relative to other poplars, aspen is thought to have high resistance to xylem cavitation (Lieffers et al. 2001). However, despite this tolerance, impairment of hydraulic function is thought to be a significant driver of drought induced mortality in aspen (Anderegg et al. 2013b).

Compared to ramets experiencing normal conditions, drought conditions have been shown to decrease water potential in aspen stems and roots leading to loss of hydraulic conductivity and increased cavitation (Anderegg et al. 2011). Loss of conductivity has been found to be much higher in drought affected trees and predictive of fine root mortality (Anderegg et al. 2011). Due to the effects of cavitation, aspen can exhibit leaf mortality at 50% loss of hydraulic conductivity and complete crown mortality at 90% loss of conductivity (Lu et al. 2010). The effects of cavitation are not irreversible, however, and can be overcome by subsequent growth and refilling of cavitated vessels. This hydraulic recovery has been observed in aspen seedlings even after complete leaf mortality due to drought (Lu et al. 2010).

This recovery mechanism indicates that the consequences of hydraulic impairment on aspen mortality is not adequately explained by the occurrence of isolated cavitation events. To test whether the effects of xylem cavitation on aspen stand health could be cumulative, Anderegg et al. (2013b), performed an observational study of SAD affected and healthy aspen stands in the San Juan national forest in Colorado. By measuring stem water potential and percent loss of conductivity in aspen branches in both stand types, they were able to compare the responses of clones that had experienced significant negative effects of drought and those that had not. They
found that although xylem water potential at predawn and midday were nearly the same for both stand types, the SAD affected ramets had a 50% loss of conductivity at -1.0 MPa compared to -2.3 MPa in healthy ramets (Anderegg et al. 2013b). The researchers also performed an experimental drought treatment by excluding rainfall in one stand during 2010 and compared the response against other stands during that year and years following. Here they discovered that midday xylem tensions were significantly greater in drought stressed ramets during the treatment year but equalized to similar tensions of the control ramets in successive years. Meanwhile, however, the droughted trees experienced significantly higher losses in conductivity during the treatment year and the two following years, reflecting similar findings to the observational study (Anderegg et al. 2013b).

These findings suggest that the effects of drought stress on aspen are cumulative and contribute to a condition known as cavitation fatigue. This condition was coined by Hacke et al. 2001 in a study involving the hydraulic physiology of six plant species, including *P. tremuloides*. Here, the researchers subjected each plant species to numerous drought stress and refilling cycles and measured the xylem tensions at which hydraulic conductivity was lost in each successive treatment (Hacke et al. 2001). While some species showed a resistance to progressive degradation of xylem function, others, including aspen, demonstrated progressively more vulnerability to cavitation with each successive treatment (Hacke et al. 2001). This cavitation fatigue results in xylem that are more permeable to air infiltration over time, possibly due to the weakening of the xylem membrane (Hacke et al. 2001).

These experiments suggest that hydraulic failure in aspen is a phenomenon that can occur over a prolonged period of repeated drought stress and can result in lasting damage to aspen
physiological processes. Since water limitations pose restrictions on growth (Lambers et al. 2008), the effects of drought on aspen could have lasting impacts on the species’ ability to persist in drought prone areas (Worrall et al. 2015). While the direct effects of water stress on aspen can be significant, drought induced mortality rarely occurs without the interacting effects of other biotic stressors (McDowell 2011). The physiological impacts of drought can significantly lower a plant’s ability to cope with biotic stressors, often considered to be the ultimate cause of mortality (Mcdowell et al. 2013). These, “secondary agents,” often effectively attack already stressed plants and can lead to mortality of the plant (Marchetti et al. 2011).

While aspen decline in the Southern Rockies was precipitated by the severe 2000 – 2003 drought (Worrall et al. 2008), the mortality of aspen in this region has since been correlated with the secondary agents of insect and fungal attacks (Marchetti et al. 2011). Marchetti et al. 2011 found much higher densities of Cytospora canker, bronze poplar borer, and aspen bark beetles in declining forests compared to healthy aspen stands in this region. The incidence of these secondary stressors was strongly correlated with recent crown loss in the unhealthy aspen stands. Since all three of these agents damage the phloem and vascular cambium of aspen, it is likely that they were partly responsible for the crown loss and declining health of the stands (Marchetti et al. 2011). A similar episode of large-scale aspen dieback was correlated to the presence of cankers and wood boring insects in aspen stands in northern Arizona (Zegler et al. 2012). This episode was also preceded by regional drought and amplified in lower elevation, moisture limited aspen stands, suggesting that drought stress contributed to crown dieback as well.
**Conclusion**

Quaking aspen occupies a unique position in western ecosystems. Supporting a high degree of biological diversity and characterized by a dynamic clonal growth habit, aspen’s unique evolutionary adaptations and complex ecological interactions render it key component of ecosystem structure and function and an important subject of ecological study. Aspen’s genetic diversity and its influence on clonal vitality and phenotypic response to environmental stressors add further nuance to our understanding of aspen. Its interdependence with multiple agents of disturbance and vulnerability to landscape scale declines raises critical questions about the ability of the species to persist in some habitat types. These questions are complicated by a lack of knowledge about long term historical aspen distribution and disturbance regimes; due to the short-lived nature of individual aspen ramets, the application of traditional dendrochronological studies of demography and fire regimes is restricted in scope (Rogers et al. 2007). Ultimately however, as a clonal species, aspen persistence may need to be contextualized over long temporal and large spatial scales where growth and decline of populations of individual ramets may not represent the persistence of the underlying aspen clone. That said, episodes of stand level dieback, such as those incited by climatic anomalies, may indicate a constriction of aspen range away from areas of topographical and edaphic vulnerability if these climatic incidents continue. These losses will inevitably result in reductions in local biodiversity and cascading effects on multiple species and ecosystem functions (Anderegg 2012a); lending urgency to the better our understanding of drivers and trends in aspen decline. As aspen research develops and evolves, we can further refine our approach to understanding the interconnections between fine
scale genetic and physiological mechanisms and large scale ecological interactions and climate forces.

Overview of Thesis

This thesis adds new information to the growing body of literature on aspen, climate and drought with a novel focus on the influence of snow cover and edaphic factors in driving drought stress in a landscape at the margin of aspen’s suitable climatic envelope. Chapter 2 describes an observational study conducted during 2017 – 2018 on The Nature Conservancy’s Zumwalt Prairie Preserve in Oregon. Very little research has been conducted or published on aspen stands in Oregon. Here aspen stands are often small and topographically confined in comparison to the sprawling aspen stands found in many parts of the North American Rockies and boreal forests of Canada. Some of Oregon’s aspen is considered to be on the edge of its range and therefore presents an ideal opportunity to study the physiological effects of atmospheric, edaphic and topographical factors as they relate to drought. We studied the associations between stand level estimates of average snow cover over a 33-year time series, stand characteristics, and spring and summer 2017 soil moisture and their connections with physiological drought stress in aspen. We also looked for direct associations between topographical, atmospheric and edaphic characteristics and physiological drought stress in aspen. By understanding the drivers of stand-level droughts stress in landscapes at the edge of aspen’s range, land managers can be better informed to anticipate and respond to the effects of climate change on these critical plant communities.
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Abstract

Quaking aspen, *Populus tremuloides*, has experienced severe declines in recent years in part due to the effects of changing climate and extreme drought. As the dominant deciduous tree in Western North American forests, aspen plays a critical role in forest biodiversity and ecosystem function. Therefore, the persistence of this species under changing climate patterns is a topic of critical concern; especially where aspen exists toward the vulnerable margin of its range. This study set out to investigate the associations of atmospheric, hydrologic, edaphic and topographic variables with physiological drought stress in aspen. The study took place on the Zumwalt Prairie in northeastern Oregon, a semi-arid bunchgrass prairie where aspen occur in isolated stands associated with riparian areas and late-season persistence of snow drifts. Using a 33-year time series of landsat imagery to detect associations of aspen stands late-season snow cover and field measurements of soil moisture in aspen stands during 2017, we found while snow dominated stands were associated with greater soil moisture during spring, levels had equilibrated to those of other upland stands by summer. Measurements of predawn and midday stem water potential in multiple height classes of aspen ramets revealed associations of both shallow soil moisture and vapor pressure deficit with physiological drought stress in aspen.
Analysis of soil texture class revealed an important association with midday stem water potential, with finer textured soils associated with somewhat higher midday drought stress than coarser textured soils. While neither topographical characteristics nor snow cover were found to be important drivers of drought stress, topographical curvature was found to have a strong influence on summer soil moisture in upland stands. These findings contribute to our understanding of aspen physiology, drought ecology and landscape hydrology toward the xeric margin of aspen’s range. This information can help land managers to anticipate and adapt to changing climates and understand their effects on key plant species such as aspen.

Introduction

*Populus tremuloides* (hereafter referred to as aspen) is the most widely distributed tree in North America (Little 1971), inhabiting a broad range of habitat types from riparian areas, meadows, shrublands, conifer forests and subalpine environments from sea level to over 3,700 ft (Debyle and Winokur 1985). Throughout the arid and semi-arid regions of the Intermountain Western US, its distribution is restricted to sites with at least 41 cm of annual precipitation, although given favorable site conditions it may persist in areas with lower annual precipitation (DeByle and Winokur 1985). Aspen is a clonal species which relies on frequent disturbance to regenerate stands by sending up clonal ramets (suckers) off of its root system (Mitton and Grant 1996). It is a critical foundation species throughout its range, providing key ecosystem structure and function in terms of pollinator diversity (Gonzalez et al. 2013), plant diversity (Kuhn et al. 2011), nutrient cycling (Buck and St. Clair 2012), avian diversity (Sallabanks et al. 2005) and hydrologic cycling (LaMalfa and Ryle 2008). Aspen also occupies an important
social and cultural space in the western landscape, providing recreational, scenic and wildlife values. Therefore, conservation of this essential species in the face of multiple stressors is of critical importance to land managers and the public.

The decline of aspen in North America as a result of conifer encroachment, herbivory, pathogens, insects and extreme climatic events has been well documented (Bartos et al. 1998; Bartos and Campbell 2001; Di Orio et al. 2005; Man and Rice 2010; Worrall et al. 2008). Since the mid 2000’s however, the influence of acute drought has received considerable attention due to its association with large and sudden incidences of aspen decline across North America (Rehfeldt et al. 2009; Michaelian et al 2011). From 2000 to 2003 a severe drought occurred across western North America characterized by record high summer temperatures, below average snow water equivalent and record low soil moisture levels (Anderegg et al. 2013a). This drought event has been linked to widespread aspen dieoff in the Rocky Mountains of Southwestern Colorado (Worrall et al. 2008), across the intermountain west and portions of the northern great lakes (Worrall et al. 2013). Furthermore, above average temperatures and record dry conditions in Western Canada between 2001 and 2002 showed a strong association with a large aspen dieoff episode in the Boreal forests of Western Canada (Hogg et al. 2008; Michaelian et al. 2011). Aspen mortality became evident within a year of these drought episodes and many stands have continued to deteriorate in successive years (Anderegg et al. 2013b; Worrall et al. 2015). In total, aspen cover declined by 3.2 million ha in North America from 2000 – 2010; bioclimate models indicate that the majority of this decline was in areas with decreased climate suitability (Worrall et al. 2013).
This drought-induced “sudden aspen decline” (SAD) as it has been termed, is characterized by branch and canopy dieback of mature trees, reduced root biomass and weak regeneration response of aspen suckers (Anderegg 2012, Worrall et al. 2010). SAD has been associated with secondary fungal pathogens and insects, as well as acute physiological drought stress leading to impaired water transport and hydraulic failure (Marchetti et al. 2011; Anderegg et al. 2013b). The latter has been attributed to a condition known as “cavitation fatigue” resulting from incidences of xylem cavitation and loss of hydraulic conductivity rendering stands more vulnerable to successive drought conditions (Anderegg et al. 2013b). Aspen’s functional reliance on shallow soil moisture may make it particularly vulnerable to drought events such as those proceeding SAD which were characterized by high evaporative demand and low soil moisture (Anderegg et al. 2013a).

Patterns of drought-induced aspen mortality have been found to be strongly influenced by topographical characteristics that may either exacerbate or mitigate the effects of heat and moisture stress (Worrall et al. 2008). In particular, aspen stands occupying south to west aspects (Huang & Anderegg 2012), lower elevations, benches and upper slope positions were disproportionately affected sudden aspen decline (Worrall et al. 2008; Worrall et al. 2015). Similar patterns were found in a separate decline episode following extreme drought where aspen mortality was higher at lower elevations, on flatter slopes and on aspects with greater heatload (Zegler et al. 2012). The effects of topography have continued to influence stand dynamics after the initial SAD episode with lower regeneration rates evident at lower elevation sites (Worrall et al. 2015). This may also be the result of feedbacks between thinning stand density and alterations in microclimates, with SAD affected stands exhibiting higher air and soil
temperatures and lower soil moisture long after initial drought events (Worrall et al. 2015). Within the low elevation areas affected most severely by sudden aspen decline, however, microsite topography has been found to buffer stands against mortality. In particular, within larger regions of topographical convergence, mortality was found to decline in along a gradient of topographical concavity, likely due to increased subsurface water availability (Tai et al. 2017). Surfaces exhibiting topographical convergence are also associated with snow accumulation, drifting and retention (Lapen et al. 1996), potentially contributing to aspen persistence in some areas by augmenting soil moisture and deterring ungulate herbivory.

It is well established that most aspen in the Western US inhabit areas that receive at least some of their annual water budget in the form of snow (Debyle 1985). This is especially true of so called “snow pocket” aspen stands, where topographical characteristics lead to greater snow accumulation and resulting subhygic conditions (slightly higher moisture relative to adjacent habitats) (Shepperd et al. 2006). Dependency on topographical characteristics may be especially important in water limited stands where snow drifting may help to protect aspen against moisture stress during drought years (Soderquist et al. 2018). The topographical characteristics of snow dependent stands may be further amplified by aspen’s deciduous habit which promotes higher snow water equivalent throughout the winter season, increasing groundwater recharge and potentially creating positive feedbacks that further promote aspen growth (La Malfa and Ryle 2008, Trimmer et al. 1984). The ecological importance of these stands cannot be overstated; they are often found within grasslands or shrublands and are a prime example of hydrologic refugia (McGlaughlin et al. 2017). Meanwhile they may be among the most vulnerable stands, given associations of recent drought-induced aspen mortality to record low snow water
equivalence (Anderegg et al. 2013a) and trends in declining late season snowpack and increasing temperatures throughout the Western US (Mote et al. 2005; IPCC 2013).

Edaphic characteristics such as soil texture have also been shown to influence drought-induced mortality of plant species (Gitlin et al. 2006). Desert plants growing in finer textured soils have been shown to exhibit higher levels of drought stress than nearby plants in coarser soils, likely due to lower plant available water at equivalent moisture levels (Sperry & Hacke 2002). These same plants demonstrated significantly lower root vulnerability to cavitation likely due to adaptation to lower soil water potential over time (Sperry & Hacke 2002). These soil-texture-drought-stress relationships have been effectively applied to modeled relationships between hydraulic safety margin and aspen mortality, effectively linking the association between fine textured soils and higher drought stress to aspen vulnerability (Tai et al. 2017).

Exceptionally high proportions of soil organic matter often found in aspen soils may also influence soil hydrologic properties and inform our understanding of drought stress in aspen.

The effects of multiple stressors often interact to influence aspen viability (Kashian et al. 2007); yet the impact of these interactions may be buffered by topographical characteristics that contribute to site resilience (Worrall et al. 2013). Stands with higher soil moisture have been associated with higher regeneration potential despite heavy herbivory pressure (Kashian et al. 2007). Total precipitation and topographical variables have been found to contribute to aspen stand resistance to conifer encroachment (Mittanck et al. 2014). Aspect, slope and elevation are likely to have influenced soil moisture resources and contributed to aspen sexual regeneration following fire (Turner et al. 2003). Steeper slopes have been associated with decreased levels of ungulate herbivory pressure (Rogers and Mittanck 2014), possibly contributing to increased
regeneration response following drought-induced decline (Zegler et al. 2012). In many cases the effects of these stressors on aspen health are strongly influenced by site characteristics that may contribute to resilience in unpredictable ways; for example, in some areas a marked increase in aspen cover on more drought prone, low elevation sites has been documented following fire (Kulakowski et al. 2004). Larger scale interactions between climate and other disturbances are also likely at play, with evidence suggesting that region wide aspen regeneration may be initiated by favorable climatic conditions following large disturbance events (Kaye 2011). Ultimately, drought-induced aspen decline may be considered a stage in a long term successional pattern, or permanent loss of a range of aspen habitat as a consequence of compounding stressors and topographical vulnerability. Under either scenario, understanding the interactions between these landscape characteristics, available soil moisture and drought stress in aspen is critical to assessing the short and long-term persistence of aspen at the landscape scale.

The objective of this study was to assess the influences of site characteristics and climatic influences on aspen drought stress by intensively investigating aspen stands in a small geographic area. Specifically, we set out to explore the linkages between snow cover, topographical characteristics, climatic factors, edaphic qualities, soil moisture and aspen physiological drought stress across snow pocket and riparian aspen stands. Our primary objectives were to: (1) Determine the strength of association between aspen stand locations and late season snow cover; (2) assess spring and summer trends in soil moisture across stand types to determine whether snow pocket or riparian stands were associated with higher summer soil moisture; and (3) assess spring and summer trends in aspen xylem water potential to determine whether soil moisture, topographical characteristics, edaphic factors or climatic variables were
driving aspen drought stress during the study period. Study locations that exist toward the xeric fringe of suitable aspen habitat may be particularly well suited for investigating these questions given continental patterns of aspen decline occurring preferentially in water and temperature limited landscapes.

Methods

Study Area

We collected data in 30 aspen stands spread across the 13,600-ha Zumwalt Prairie Preserve (ZPP) owned by The Nature Conservancy (TNC) in NE Oregon. Located in the Blue Mountains ecoregion, the ZPP occupies a substantial portion of the larger Zumwalt Prairie, a 64,000-ha grassland that represents the largest remaining fragment of Pacific Northwest Bunchgrass prairie (Tisdale 1982).
Figure 1: Map showing the location of the study area within the Blue Mountains ecoregion in the NE corner of Oregon.

Largely characterized by high grass and forb diversity, the Zumwalt Prairie also sustains pockets of highly productive mesic aspen and shrub communities where topographic characteristics facilitate favorable edaphic qualities and soil moisture resources. Commonly associated shrub species found in these habitats include *Amalanchier alnifolia*, *Symphorocarpus albus*, *Crataegus douglasii*, *Prunus virginiana* and *Physocarpus malvaceous*, with the conifer species *Pinus ponderosa* and *Pseudopstsuga menzesii* encroaching into some of the stands. Aspen stands on the ZPP are primarily found on slopes of north and east aspects where snow
drifts persist into the spring season (hereafter referred to as upland stands), or alternatively, along riparian corridors fed by perennial or intermittent streams (hereafter referred to as riparian stands). From 1976 to 2001, total aspen cover on the Zumwalt Prairie declined from 7.2 ha to 5.9 ha likely due to a combination of factors including herbivory, drought, fire suppression and conifer encroachment (Bartuszevige et al. 2012). Evidence of decadent and declining aspen stands on the Zumwalt Prairie Preserve led to the construction of exclosures for the purpose of fencing out native ungulates and livestock thought to be damaging several of the stands (Taylor and Arends 2011). While these efforts have been successful in promoting aspen release in several stands (Taylor and Rossman 2013), evidence of canopy mortality and differences in regeneration and recruitment response has raised questions about the influence of drought stress on stand viability (Appendix C, Figure C.1).

The relatively shallow soils of the Zumwalt Prairie Preserve have largely precluded crop production and consequently livestock grazing is the predominant land use (Bartuszevige et al. 2012). The soils on the preserve are primarily Xerolls of loamy texture classes and include argillic subsurface horizons (Soil Survey Staff 2012). Soil parent material is largely composed of loess deposited after Pleistocene glaciation and Columbia river basalt colluvium, with influences of volcanic ash evident in many soils (Soil Survey Staff, 2012; Soil Survey Staff, 2018).

The climate of the Zumwalt Prairie Preserve is characterized by cold, wet winters and warm, dry summers. According to data collected on site at the Zumwalt weather station between 2006 and 2017, the ZPP averages 36cm of annual precipitation with only 5cm falling during the
summer months (July - September) and average temperatures ranging from -2.9° C during the winter months (December – February) to 15.7° C during the summer months (Table 4).

The sampling protocols described herein were repeated across five, five-day sampling periods in May, June, July, August and September of 2017. Sampling periods occurred toward the middle of each month and were spaced 28 days apart. Soil moisture was sampled in each of the 30 stands; xylem water potential and soil physical properties were measured on a subset of 16 of the stands. These 16 focal stands were selected randomly in proximal clusters while considering representation across a range of three criteria; ungulate exclosure status; availability of adequate trees for sampling (n=22); and association with either riparian areas or upland landscape positions (Appendix A, Table A.1).

**Soil Moisture Sampling**

Grids of regularly spaced soil moisture sampling points were generated within previously mapped aspen stand polygons using ArcGIS 10.5. The number of grid points was allocated proportional to stand size to ensure that each stand had a representative number of sampling points (Appendix A, Table A.2). The number of sampling points per stand is variable for some stands in May, June and July since grids were not standardized until the July sampling round. Sampling points were navigated to using a handheld GPS device or a smart phone using IGis (Geometry Pty Ltd. 2018). Soil moisture was measured using a Campbell Scientific Hydrosense 2 soil moisture probe with a 20 cm probe tip which measures % volumetric water content (VWC), expressed in cm³/cm³. GPS accuracy allowed for a measurement accuracy of within 3 m of each sampling point and care was taken to avoid sampling in disturbed soil from previous sampling rounds. Rocks, roots, and animal burrows were also avoided during sampling and
alternative points were randomly selected within 1 m from where these features occurred. Surface horizon, 0 - 20 cm moisture values were recorded by first removing surface vegetation then inserting the probe into the soil. To record moisture at 20 - 40 cm soil depths, 20 cm deep holes were excavated at each sampling point. In focal stands, these measurements were taken within one day of drought stress measurements to ensure fidelity between the two variables.

**Continuous Data Collection**

In order to measure trends in soil moisture in finer temporal resolution across the season, in June of 2017, six Campbell Scientific 655 reflectometer probes were installed in Aspen Stand 1 and connected to a CR1000 datalogger (Appendix C, Figure C.2). Three locations within 4 m of each other were chosen for installation; just underneath the canopy of one mature aspen ramet; just underneath the canopy of two small ponderosa pine trees; and within a small grove of aspen ramets. In each location, soil pits were excavated to 75cm and two probes were installed horizontally at 40 cm and 70 cm. Soil samples were collected for texture analysis and probe calibration from each pit at each depth.

Weather data was collected from the Zumwalt Prairie weather station (ZumWxStn) located at the center of the preserve. This station is within 2 km of all of the stands and provides hourly data on temperature, precipitation and relative humidity. Temperature and relative humidity data were used to calculate daily and hourly vapor pressure deficit (VPD) following equations 7, 11 and 14 provided in Walter et al. 2005. Vapor pressure deficit takes into account temperature and relative humidity and provides a measure of the drying effect of air on plants. Weather data from 1910 – 2017 was also collected from the PRISM dataset to compare against ZumWxStn values (Daly et al. 1997).
Drought Stress Sampling

Drought stress was estimated by measuring stem water potential in aspen twigs. Stem water potential measured during the midday period (12:00 – 14:30) can provide a useful measurement of drought stress during high evaporative demand (Chone et al. 2001) and a more sensitive measurement of small differences plant water status than leaf water potential (McCutchan et al. 1992). Likewise, stem water potential measured during predawn periods (2:30 - 5:00 AM) provides an indication of plant water status when transpiration is null and therefore is often correlated with soil water status (Chone et al. 2001). While stem water potential is less variable than water potential measured in leaves (McCutchan et al. 1992), it is nonetheless highly variable across time (different times of day, from one day to the next, from one month to the next), across space (vertically throughout a tree canopy, across topographic gradients and between tree height classes). Consequently, to reduce variability across time, sampling periods were condensed into five-day windows thereby limiting the number of stands possible for sampling to 3 – 4 per day. Due to the short time window, stands in close proximity were sampled during the same day. Each of these stand clusters were sampled on the same day during each sampling round (i.e. the cluster with stands 1, 2 and 8 was sampled on day one of each round) however, within clusters, stands were sampled in random order to avoid systematic error associated with changing water potential across each time window.

For drought stress measurements, sampling points within stands were randomly selected from grids created for soil moisture sampling. To attain a representative measure of spatial variability across each stand and to avoid the cumulative effects of destructive sampling on individual trees, a different point was chosen for each sampling round. From these points, trees
were randomly selected for two of three height classes, sucker (<2m), juvenile (≥2m <5m), and mature (≥5m). For each stand, two trees of the tallest height class present (either juvenile or mature) were randomly selected and three to five suckers were chosen haphazardly near the tall trees. See appendix A, table A.3 for a breakdown of height classes sampled for each stand. For each height class sampled, ten twigs were collected throughout the tree canopies, for a total of ten twigs per height class. For the tall trees, a 6m polesaw and a Big Shot tree sling shot were used for canopy sampling. Twigs were immediately misted with water and bagged in airtight plastic bags placed in a larger opaque sack. Twigs were left bagged for at least 5 minutes in order for stem water potential to come into equilibrium with the xylem, following Anderegg 2012. Within each stand, trees were sampled during the period of minimum drought stress (predawn, 2:30 to 5:00) then revisited in the same day during peak drought stress (midday, 12:00-14:30). Predawn twigs were transported to a vehicle and sampled within 90 minutes of collection, midday twigs were sampled on site within 15 minutes of collection. Each of these was measured for xylem water potential, expressed in MPa, using a Scholander pressure chamber (PMS Instruments, Albany, OR). Height of all trees (except during the May sampling round) was measured using a laser range finder and clinometer, the MOTI timber cruising smartphone app (Rosset 2014) or a rigid ruler.

**Soil Depth and Soil Physical Characteristics Sampling**

Soil depth was measured in each of the 16 focal stands. Between four and six points were randomly selected for depth measurements according to stand size using moisture sampling grids established previously. At each point, depth was measured at 3 m from a center point at 0, 90, 180 degrees by pounding a 75 cm probe into the soil until reaching the maximum probe
depth or bedrock. In each stand, soil at 0 – 20 cm and 20 – 40 cm was sampled at a subset of these locations for texture analysis. Soil samples at each depth were collected at two points for stands of less than 0.5 acres in size; four points for stands of between .05 and 2 acres in size and six points for stands of greater than 2 acres (Appendix A, Table A.2).

Soil samples were transported to the lab, air dried, then combined and mixed for each stand in preparation for analysis of physical texture and organic matter content. For fine fraction texture analysis (<2mm particle size), 50g subsamples were weighed and organic matter was removed from each using an (H₂O₂) solution prior to texturing. Samples were then processed using the hydrometer method as described by Ashworth et al. 2001 (Appendix C, Figure C.3). Three replicate measurements were taken for each sample and averaged for each soil depth within each stand to determine % by volume (ml) of sand, silt and clay. For each depth within each stand, approximately 730 - 1000g was used for coarse fragment analysis. Coarse fragments were cleaned, sieved and weighed to determine % of fine gravels (≥ 2mm ≤ 4.75 mm), medium gravels (≥ 4.76 ≤ 19mm) and coarse gravels (≥ 20mm) by weight (g). Organic matter content was analyzed using the loss on ignition technique following (Gavlak et al., 2000) to determine % soil organic matter by weight (g) for each sample.

**Remote Sensing Imagery Analysis**

A remote sensing imagery analysis was performed to assess the strength of association between late season snow cover and aspen stands. A collection of 355 Landsat images taken during the months of March through May from 1984 to 2017 were used in analysis. These were orthorectified images from the Landsat 5 and 8 satellites preprocessed by USGS using top of atmosphere reflectance (Chander et al. 2009). All images were high quality Level L1T scenes
from the TM and ETM+ sensors at 30 m spatial resolution. Images were available at 8-day
temporal resolution due to the Zumwalt Prairie Preserve’s location at the overlapping edge of
two Landsat path rows. Images were unavailable during May of 2012 and March of 2013
between the decommissioning of Landsat 5 and the initiation of Landsat 8.

This USGS collection was preprocessed for normalized difference snow index (NDSI)
(Riggs et al., 1994). NDSI provides a useful tool for identifying snow cover on the landscape
using the Green and Mid Infrared spectral bands of the Landsat 5 TM sensor and the Green and
Shortwave Infrared spectral bands of the Landsat 8 OLI sensor (Crawford et al. 2013, Sibadze et
al 2014). Since snow exhibits high reflectance in the visible green portion of the electromagnetic
spectrum and low reflectance in the mid and shortwave infrared, a simple ratio can be used to
identify snow while simultaneously distinguishing it from cloud cover:

\[
NDSI = \frac{\text{Green band} - \text{IR band}}{\text{Green band} + \text{IR band}}
\]

Analysis of these images was performed in Google Earth Engine (Gorelick et al. 2017)
(Appendix C). Aspen stand boundaries were imported from ArcGIS and NDSI values were
calculated for each stand for each image. NDSI ranges from -1 to 1 and values above a threshold
of 0.4 reliably indicate greater than 50% snow cover for a given pixel (Hall et al. 1998, Dietz et
al. 2012). Using this threshold, total snow-covered area was calculated for each stand in each
image. These values were then averaged across the time series for each stand and divided by the
stand area to generate a proportion of snow covered area across the stand from March through
May (P\text{snow}) and April through May (P\text{snowAM}) between 1984 and 2017 (see equation below).
Pixels that intersected the stand boundaries were included in the calculation effectively buffering
each stand to include a slightly larger area of the landscape. This is an ecologically sound
approach considering the likelihood that snow cover in the area immediately surrounding each stand would contribute to stand level soil moisture. The same process was used to calculate the proportion of snow cover area across the upland portion of the ZPP during the same period to determine the relative snow cover of aspen stands compared to the entire upland portion of the ZPP.

P_{\text{snow}} \text{ equation:}
\[ \frac{\sum S_{ti}}{A_t} \frac{355}{n} \]

Where:
\[ S = \text{the snow covered area in m}^2 \text{ within the mapped perimeter of each object of interest } t \]
for each image \( i \) from March – May 1984 - 2017 (n = 355)
\[ A = \text{total area of the object of interest } t \text{ in m}^2 \]
\[ t = \text{object of interest (individual aspen stand or upland ZPP)} \]

Geospatial Analysis

Topographical attributes of each stand were derived using ArcGIS 10.5 from 1/3 arc second digital elevation models accessed from the USGS national elevation dataset (USGS 2015). Using previously GPS mapped stand boundaries, average values were calculated for slope, aspect, elevation, profile curvature, planform curvature, standard curvature and compound topographic index, a measure of topographically driven soil wetness (Gessler et al. 1995).

Data Description and Limitations

Prior to analysis, soil moisture and water potential datasets were filtered for outlier values. While care was taken to avoid sampling unhealthy aspen stems, some water potential
measurements during August and September were taken on trees that were afflicted by black leaf spot caused by infection of the fungus *Marissonina populi* (Lib). This foliar disease can result in smaller leaves, tissue desiccation and can lead to mid-summer defoliation of the trees (Hinds 1985). Water potential values taken from afflicted trees in Stand 1 during August were removed from the all analysis because of their abnormally high values; additionally, measurements taken in Stands 2 and 14 during September were removed from predawn drought stress models. To further account for measurement error in pressure chamber use and sampling error in twig selection, water potential measurements were filtered using Tukey’s rule. For each set of 10 twig samples within each month/stand/height class/time of day, values outside of 1.5 times the interquartile range were identified as outliers and removed. In total, 129 outliers were removed from an original dataset of 3069 samples. Soil moisture measurements taken in saturated riparian soils directly adjacent to creeks were removed from the dataset since they represented uncommonly high soil moisture levels where aspen were not present. Additionally, to account for sampling error due to the presence of rocks or other unrepresentative conditions, soil moisture values were filtered using Tukey’s rule within each month/stand/depth set of measurements. In total, 97 outliers were removed from an original dataset of 3560 soil moisture measurements.

Stem water potential measurements for each time of day were averaged for each height class, yielding four values per stand per month (n=160). Of the 16 stands sampled for water potential, two contained only trees of the sucker height class with no juvenile or mature trees sampled. Soil moisture measurements from 0 – 20 cm and 20 – 40 cm depths were averaged for each stand, yielding two values per stand, per month (n=300). Due to a navigation error, soil
moisture values were not recorded in stand 14 during the month of May, these values were later predicted and added to the dataset using a general linear model accounting for soil moisture trends across the season and average values during May.

**Statistical Analysis Overview**

Data was analyzed using a combination of generalized least squares and linear mixed models. Generalized least squares models were used to analyze data that had been averaged for the entire season or a portion of the season, whereas linear mixed models were used to analyze data averaged for each month and therefore detect patterns across the season. Generalized least squares models allowed us to account for patterns of residual correlation by modelling non-constant variance across predictor variables. Linear mixed models allowed us to account for the effects of non-independence and residual correlation by incorporating temporal correlation structures and random effects into our models. Each full model was fit using maximum likelihood followed by stepwise model selection on each of the models to determine which set of fixed effects had the greatest support using bayesian information criterion (BIC). BIC is widely considered to be a more consistent criterion than AIC and one which often leads to more parsimonious models by taking into account the number of observations involved (DeLuna et al. 2003). Upon selection of the final fixed and random components for each model, all models were inspected for outliers and validated by testing assumptions of normality, homogeneity and independence of residuals. Marginal f-tests were used to assess the statistical significance of each predictor and any interaction terms included in the final models. Confidence intervals and linear contrasts were generated using the R package ‘lsmeans’ (Lenth 2016). All pairwise comparisons are reported with Bonferroni adjusted 95% confidence intervals to account for
increased type 1 error rates when performing multiple comparisons. Paired t-tests were used in some limited circumstances to compare groups outside of mixed models and are indicated in the results.

**Upland Soil Moisture Modeling**

Two generalized least squares models were used to assess the effects of topographical characteristics and late season snow cover on soil moisture for upland stands (n = 24). Soil moisture analysis was divided into two distinct seasons, May through June (late spring) and July through September (summer) based on an abrupt decline in soil moisture between June and July (Figure 7). Analyzing these periods separately allowed us to get at potentially shifting soil moisture dynamics during a period of abundant moisture in late spring and of limited moisture in summer. Additionally, this allowed for more parsimonious models given a small sample size. Mean average soil moisture (% volumetric water content) was the response variable for both models. For the late spring soil moisture model (SmSpring), soil moisture values were averaged for each depth (0 – 20 cm and 20 – 40 cm) for each upland stand across the May and June sampling rounds (n = 48). The same was done for the summer soil moisture model (SmSummer) for the July, August and September sampling rounds (n=48). Both models began with the same stand level predictor variables for model selection: Depth (a two-level factor indicating soil moisture measurement depth), Topo (a two-level factor indicating upland or uplandSnow stand types), Slope (degrees), Aspect (radians), Elevation (meters), Planform curvature, Profile curvature, Compound topographic index, Psnow (average percent cover of snow from March – May), and PsnowMA (proportion of snow covered stand from April – May) (Table 1).
Table 1: Predictor variables included in model selection for generalized least squares and linear mixed models. All values were stand level averages. Predictors were initially selected for each model by assessing linear correlations with response variables. Models described: MD – Midday drought stress models; PD – Predawn drought stress models; All SM – All upland soil moisture models; SmSummer – July to September soil moisture; SmSpring – May to June soil moisture; s – sucker height class model; t – juvenile and mature height class model; av – average height class model.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Type</th>
<th>Description</th>
<th>Included in:</th>
</tr>
</thead>
<tbody>
<tr>
<td>SM</td>
<td>Soil Moisture</td>
<td>Soil moisture averaged across 0 – 40 cm depth (%VWC)</td>
<td>All MD, All MD</td>
</tr>
<tr>
<td>SM_20</td>
<td>Soil Moisture</td>
<td>Soil moisture measured at 0 – 20 cm depth (%VWC)</td>
<td>All PD, All PD</td>
</tr>
<tr>
<td>SM_40</td>
<td>Soil Moisture</td>
<td>Soil moisture measured at 20 – 40 cm depth (%VWC)</td>
<td>-</td>
</tr>
<tr>
<td>VPDh</td>
<td>Weather</td>
<td>Average vapor pressure deficit during the hour of water potential sampling (kpa)</td>
<td>All MD, All MD</td>
</tr>
<tr>
<td>VPD1</td>
<td>Weather</td>
<td>Average vapor pressure deficit during the day preceding water potential sampling (kpa)</td>
<td>All PD, All PD</td>
</tr>
<tr>
<td>Month</td>
<td>Temporal</td>
<td>Sampling month: May, June, July, August, September.</td>
<td>All MD, All PD</td>
</tr>
<tr>
<td>Topo</td>
<td>Topographic</td>
<td>Aspen habitat types: upland, uplandsnow, riparian.</td>
<td>All MD, All PD, All SM</td>
</tr>
<tr>
<td>Aspect</td>
<td>Topographic</td>
<td>Folded aspect (radians)</td>
<td>All MD, All PD, All SM, MDs</td>
</tr>
<tr>
<td>Slope</td>
<td>Topographic</td>
<td>Slope (degrees)</td>
<td>All MD, All PD, All SM</td>
</tr>
<tr>
<td>Elev</td>
<td>Topographic</td>
<td>Elevation (m)</td>
<td>All MD, All PD, All SM</td>
</tr>
<tr>
<td>CurvS</td>
<td>Topographic</td>
<td>Standard curvature (unitless)</td>
<td>-</td>
</tr>
<tr>
<td>CurvPro</td>
<td>Topographic</td>
<td>Profile curvature (unitless)</td>
<td>All MD, All PD, All SM, SmSummer</td>
</tr>
<tr>
<td>CurvPlan</td>
<td>Topographic</td>
<td>Planform curvature (unitless)</td>
<td>All MD, All PD, All SM, SmSummer</td>
</tr>
<tr>
<td>Psnow</td>
<td>Topographic</td>
<td>Percent cover of snow from March - May</td>
<td>All MD, All PD, All SM</td>
</tr>
<tr>
<td>PsnowMA</td>
<td>Topographic</td>
<td>Percent cover of snow from April - May</td>
<td>All MD, All PD, All SM</td>
</tr>
<tr>
<td>CTI</td>
<td>Topographic</td>
<td>Index of topographical soil wetness (unitless)</td>
<td>All MD, All PD, All SM</td>
</tr>
<tr>
<td>TCL</td>
<td>Soil</td>
<td>Texture classes: Silty Clay and Silty Clay Loam</td>
<td>All MD, All MD, MDt, MDav</td>
</tr>
<tr>
<td>AWC</td>
<td>Soil</td>
<td>Available water holding capacity</td>
<td>All MD, All PD</td>
</tr>
<tr>
<td>Sand</td>
<td>Soil</td>
<td>% by volume of fine earth fraction (&lt;2mm) after organic matter removal</td>
<td>All MD, All PD</td>
</tr>
<tr>
<td>Silt</td>
<td>Soil</td>
<td>% by volume of fine earth fraction (&lt;2mm) after organic matter removal</td>
<td>All MD, All PD</td>
</tr>
</tbody>
</table>
Table 1: (Continued)

<table>
<thead>
<tr>
<th>Clay</th>
<th>Soil</th>
<th>% by volume of fine earth fraction (&lt;2mm) after organic matter removal</th>
<th>All MD, All PD</th>
<th>-</th>
</tr>
</thead>
<tbody>
<tr>
<td>SOM</td>
<td>Soil</td>
<td>% by weight soil organic matter of the fine earth fraction</td>
<td>All MD, All PD</td>
<td>-</td>
</tr>
<tr>
<td>Gravel</td>
<td>Soil</td>
<td>% by weight of the coarse fraction (≥2mm) of the entire soil sample</td>
<td>All MD, All PD</td>
<td>-</td>
</tr>
</tbody>
</table>

Prior to model selection, predictor variables were assessed for patterns of correlation and potential outlier effects by plotting each one against SM. Multicollinearity was assessed, and predictors were removed above a variance inflation factor (VIF) value of four, a moderate threshold (Zurr et al. 2011). Due to high VIF, the snow variables (Psnow, PsnowMA and Topo) were included separately in three models with the remaining covariates. Elevation was removed from all models due to high VIF in association with the snow variables. Once predictor variables were chosen, each of the three resulting models was visually assessed for homogeneity of variance across each predictor using standardized residuals. If heterogeneity was detected, models were fit using restricted maximum likelihood and different variance structures were tested to determine the optimal model using BIC (Zurr et al. 2011). Upon selecting a final model for spring (SmSpring) and summer (SmSummer) each was validated as described in the “Statistical Analysis Overview” section.

**Drought Stress Modelling**

Linear mixed models were used to assess associations between both midday and predawn drought stress, measured in stem water potential (MPa), and predictor variables (Table 1) for different height classes of aspen trees across the focal stands (n=16) during the summer season (July – September). We chose to focus our drought stress analysis on the three summer months sampled, given that this is when the patterns of drought stress would have the greatest
physiological consequences and therefore ecological relevancy. All drought stress models used values for water potential averaged for each stand for each sampling month of interest (n=48 total). Three models were used for each day period (predawn and midday); one using water potential measurements on aspen suckers (<2m height) (n=48); one using average water potential measurements across height classes (n=42); and another which grouped together juvenile (≥2m <5m) and mature aspen (≥5m) (n=42). Juvenile and mature aspen were grouped together due to low sample size and biological similarity in comparison to the sucker aspen height class. Two stands (stands 24 and 25) only contained sucker height class aspen so these stands were not included in the average or mature models.

Predictor variables were initially selected using linear correlations with either midday or predawn water potential across the summer season. Full models were then assessed for multicollinearity and predictors were removed past a VIF threshold of 15. SM was included in all models due to the interest in estimating its associations with drought stress, yet SM demonstrated relatively high VIF in association with Month, potentially inflating standard errors (Dormann et al. 2013). Many variables in these repeated measures analyses were excluded due to high multicollinearity, especially soil variables which share considerable information due to their compositional nature (Dormann et al. 2013). For this reason, during final model selection, the group of predictors for midday models included only SM, VPDh, Topo, TCL, Aspect, and Gravel; and predawn models predictors included only SM, VPD1, Topo, TCL, Aspect, CurvPro and CurvPlan (Table 1). All models included a random effect for StandID to account for lack of independence between repeated measurements taken in the same stand during each month of sampling. Other random effects were tested including those that accounted for stands nested
within sampling rounds, yet the stand level random effect was consistently the best by BIC. Following random effect selection, full models including all predictors, relevant interactions and the stand level random effect, were fit with multiple different temporal correlation structures to account for residual correlation within and between sampling months, and variance structures to account for nonconstant variance across predictors, then assessed for model fit using BIC (Zurr et al. 2011). Top models were then assessed using stepwise model selection to determine final fixed effects. All models included Month as a categorical fixed effect to account for the inherent variability in stem water potential between months.

Results

Geospatial Analysis

The 30 aspen stands spread across the Zumwalt Prairie Preserve occupy a relatively narrow set of topographical positions and habitat characteristics, yet some differences are evident (Table 2). ZPP aspen stands span an elevational gradient of 211 m, occupying elevations from as low as 1380 to as high as 1591 m. Aspects are confined from north to east aspects with one stand occupying a northwest aspect. Slopes are more variable with flatter riparian stands occupying slopes angles as low as 3.98 degrees and upland stands occupying slope angles as high as 24.92 degrees. Aspen stands are generally found in areas of concave topographical curvature (Table 2).
Table 2: Aspen stand characteristics across the Zumwalt Prairie Preserve. Shading indicates focal stands measured for drought stress. Topo indicates aspen habitat type. Psnow is the average % cover of snow from March - May from 1984 – 2017. PsnowAM is the average % cover of snow from April - May from 1984 – 2017. Slope is in degrees. AspectCls refers to aspect class and is provided for reference, whereas folded aspect was used for analysis. Elev. is elevation in meters above sea level. CurvPlan and CurvPro are unitless indices of planform and profile surface curvature.

<table>
<thead>
<tr>
<th>Stand</th>
<th>Topo</th>
<th>Psnow</th>
<th>PsnowAM</th>
<th>Slope</th>
<th>AspectCls</th>
<th>Elev.</th>
<th>CurvPlan</th>
<th>CurvPro</th>
</tr>
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<tbody>
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<td>1</td>
<td>Upland</td>
<td>7.6%</td>
<td>4.2%</td>
<td>21.92</td>
<td>45 NE</td>
<td>1432</td>
<td>-0.35</td>
<td>0.21</td>
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<tr>
<td>2</td>
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<td>-0.32</td>
<td>0.22</td>
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<td>3</td>
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<td>8.4%</td>
<td>4.8%</td>
<td>5.91</td>
<td>45 NE</td>
<td>1449</td>
<td>-0.22</td>
<td>0.22</td>
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<td>-0.11</td>
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<td>4.5%</td>
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<td>3.9%</td>
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<td>4.2%</td>
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<td>5.5%</td>
<td>21.28</td>
<td>45 NE</td>
<td>1539</td>
<td>0.08</td>
<td>0.33</td>
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<td>10</td>
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<td>5.1%</td>
<td>22.24</td>
<td>45 NE</td>
<td>1528</td>
<td>-0.10</td>
<td>0.18</td>
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<tr>
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<td>7.1%</td>
<td>4.4%</td>
<td>22.78</td>
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<tr>
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<td>4.4%</td>
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<td>10.67</td>
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<td>1415</td>
<td>1.08</td>
<td>0.26</td>
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</table>
Table 2: (Continued)

<table>
<thead>
<tr>
<th></th>
<th>UplandSnow</th>
<th>P_{snow}</th>
<th>P_{snowAM}</th>
<th>Date</th>
<th>NO</th>
<th>Score</th>
<th>Chipmunk</th>
</tr>
</thead>
<tbody>
<tr>
<td>28</td>
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<td>5.4%</td>
<td>12.75</td>
<td>00 NO</td>
<td>1502</td>
<td>-0.29</td>
<td>0.11</td>
</tr>
<tr>
<td>15a</td>
<td>12.4%</td>
<td>5.5%</td>
<td>14.14</td>
<td>00 NO</td>
<td>1509</td>
<td>0.00</td>
<td>0.41</td>
</tr>
<tr>
<td>15b</td>
<td>12.8%</td>
<td>5.4%</td>
<td>11.87</td>
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<td>1516</td>
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<td>0.22</td>
</tr>
<tr>
<td>15c</td>
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<td>5.1%</td>
<td>11.94</td>
<td>00 NO</td>
<td>1522</td>
<td>-0.04</td>
<td>0.53</td>
</tr>
</tbody>
</table>

**Snow Analysis**

Across the 33-year time series from 1984 to 2017, aspen stands across the ZPP averaged 9.4% snow cover (range 6.7% - 12.9%) (Table 2). By comparison, the entire upland portion of the ZPP averaged 4.9% snow cover during the same period (Figure 3). This confirms anecdotal evidence of a strong association of aspen stands with snow cover on the ZPP. More importantly, this allowed us to analyze the relative strength of the association between snow and aspen habitat across the prairie during the study period. From these analyses, a clear demarcation between upland stands with a P_{snow} above or below 9.5% (or P_{snowAM} of 5%) was evident, leading us to classify upland stands into two categories, upland (P_{snow} < 9.5%, n=12) and uplandSnow (P_{snow} ≥ 9.5%, n=13) (Figure 2).

![Figure 2](image_url)

**Figure 2:** Distribution and classification of upland habitat types on the Zumwalt Prairie Preserve according to average percent snow cover from 1984 – 2017. A: March – May snow cover (P_{snow}). B: March – May snow cover (P_{snowAM}). Upland stands with an average of ≥ 5% P_{snowMA}, or ≥ 9.5% P_{snow} were classified as uplandSnow stands.
Figure 3: Average March – May snow cover across the Zumwalt Prairie Preserve from 1984 – 2017 showing aspen habitat types and their association with late season snow cover. This map was generated using 4-year averages (due to challenges in iterating processes in Google Earth Engine) whereas the actual snow analysis was based on single year averages. For this reason, the map indicates much higher average values but is still useful for illustration purposes.

Of the 355 images processed for snow cover, 92 contained pixels with detectable NDSI values within aspen stands. This number would have likely been higher if it were not for frequent cloud cover during months covered by the analysis. While NDSI can effectively distinguish light cloud cover from snow, heavy cloud cover would have obscured the ground
surface and led to non-detectable NDSI values. For this reason, our estimates of snow cover are likely conservative, but are still useful for comparing among aspen habitat types and between aspen habitats and the greater upland portion of the ZPP. This fact also precluded the possibility of analyzing trends in changing snow cover across the 33-year period since detection of snow cover may be confounded with presence or absence of heavy cloud cover.

Soils

In 13 of the 16 aspen stands sampled, median soil depth was deeper than 75 cm, with three stands having soils with a median depth of 46 cm or deeper (Table 3). A longer depth probe would have allowed more precision in measuring deeper soils, but in comparison to estimated average soil depths across the entire study area (52 cm), soils in these stands are generally deeper than the surrounding area (Soil survey staff 2018). Based on texture values from the upper 40 cm of the soil surface, all 16 focal aspen stands had either clay loam (n=9) or silty clay loam (n=7) texture classes. We found very high soil organic matter across stands, especially in the upper 20 cm of soil. Soil organic matter by weight averaged 12.9% (+/- 2.5) in the upper 40 cm of soil; 14.2% (+/- 2.7) in the upper 20 cm; and 11.6% (+/- 2.6) in the 20 – 40 cm depth (means +/- SD). These values are considerable higher than estimates of average soil organic matter in the upper 40 cm of the soil surface across the study area (7.4%) (Soil survey staff 2018). Gravel content was highly variable across stands, ranging from 1 – 22% by weight in the upper 40 cm of soil surface and averaging 11.4% (+/- 6.7) in the upper 40 cm of soil; 10.7% (+/- 6.7) in the upper 20 cm; and 12.1% (+/- 7.1) in the 20 – 40 cm depth (means +/- SD). All of these components are influential in determining the available water content of the soil which ranged from 15.2 to 20.7 cm²/cm² in the 0 - 40 cm horizon; averaging 17.3 cm²/cm² (+/-
1.7) in the 0 - 40 cm horizon; 17.0 cm$^2$/cm$^2$ (+/- 1.7) in the 0- 20 cm horizon and 17.5 cm$^2$/cm$^2$ (+/- 1.9) in the 20 – 40 cm horizon (means +/- SD) (Table 3).

Table 3: Soil characteristics for focal aspen stands on the Zumwalt Prairie Preserve. All values given are for the upper 40 cm of the soil surface with the exception of depth. Soil texture class (TCL) is grouped into silty clay loam (SiCL) and clay loam (CL). Sand, silt and clay are expressed as a percentage by volume of the fine earth fraction of the soil (<2mm) after organic matter removal. Soil organic matter (SOM) is percent by weight of the fine earth fraction. Gravel is the coarse fraction (≥2mm) percent by weight of the entire soil sample including the fine earth fraction and soil organic matter. Available water content is the percentage of plant available water. Soil depth is median soil depth to a restrictive layer in cm.

<table>
<thead>
<tr>
<th>StandID</th>
<th>TCL</th>
<th>Sand</th>
<th>Silt</th>
<th>Clay</th>
<th>SOM</th>
<th>Gravel</th>
<th>AWC</th>
<th>Depth</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>SiCL</td>
<td>20%</td>
<td>45%</td>
<td>35%</td>
<td>13%</td>
<td>11%</td>
<td>16%</td>
<td>&gt;75</td>
</tr>
<tr>
<td>2</td>
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<td>23%</td>
<td>46%</td>
<td>31%</td>
<td>14%</td>
<td>4%</td>
<td>19%</td>
<td>&gt;75</td>
</tr>
<tr>
<td>3</td>
<td>CL</td>
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<td>46%</td>
<td>33%</td>
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<td>4%</td>
<td>17%</td>
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<td>10%</td>
<td>20%</td>
<td>&gt;75</td>
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<tr>
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<td>17%</td>
<td>&gt;75</td>
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<td>32%</td>
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<td>SiCL</td>
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<td>48%</td>
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<td>22%</td>
<td>15%</td>
<td>56</td>
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<td>12%</td>
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<td>17%</td>
<td>&gt;75</td>
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<td>34%</td>
<td>10%</td>
<td>20%</td>
<td>16%</td>
<td>&gt;75</td>
</tr>
</tbody>
</table>
Climate

The 2016 – 2017 winter proceeding the sampling period was characterized by an anomalously cold winter with above average snowfall for the region (Allen and Murphy, 2017). Weather was generally average during the 2017 sampling period with the notable exception of warm temperatures and low humidity during summer (Figures 3 and 4). During the entire sampling period from May to September of 2017, temperatures were 0.6º C above average and precipitation was 39 cm below average, yet both were within one standard deviation of the 2006 - 2017 mean (Table 4, Figures 3 and 5). Vapor pressure deficit during the study period was significantly above average (0.15 kpa) (Table 4, Figure 4). Temperature, vapor pressure deficit and precipitation were average during spring of 2017. During summer, however, while precipitation was average, temperature and vapor pressure deficit were significantly above average (0.9º C and 0.21 kpa respectively) (Table 4, Figures 3, 4 and 5).

Table 4: Weather data recorded at the Zumwalt Weather Station from 2006 – 2017 averaged for four periods. Bold numbers for the 2017 study season indicate where values fall outside of one standard deviation of average values from 2006 – 2017.

<table>
<thead>
<tr>
<th>Season</th>
<th>Temp (C)</th>
<th>VPD (kpa)</th>
<th>Precip (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>Annual</td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>2006 - 2017</td>
<td>5.97</td>
<td>± 0.63</td>
<td>0.67</td>
</tr>
<tr>
<td>2017</td>
<td>5.84</td>
<td>-</td>
<td>0.72</td>
</tr>
<tr>
<td>Study Period (May – Sept)</td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>2006 - 2017</td>
<td>13.60</td>
<td>± 0.81</td>
<td>1.17</td>
</tr>
<tr>
<td>2017</td>
<td>14.26</td>
<td>-</td>
<td><strong>1.32</strong></td>
</tr>
<tr>
<td>Spring (April – June)</td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>2006 - 2017</td>
<td>8.18</td>
<td>± 1.23</td>
<td>0.66</td>
</tr>
<tr>
<td>2017</td>
<td>8.33</td>
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<td>0.67</td>
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Table 4: (Continued)

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<tr>
<th>Summer (July – Sept)</th>
<th>Mean</th>
<th>SD</th>
<th>Mean</th>
<th>SD</th>
<th>Mean</th>
<th>SD</th>
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<tbody>
<tr>
<td>2006 - 2017</td>
<td>15.75</td>
<td>± 0.85</td>
<td>1.43</td>
<td>± 0.14</td>
<td>48.83</td>
<td>± 29.18</td>
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<td>2017</td>
<td>16.62</td>
<td>-</td>
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<td>-</td>
<td>28.70</td>
<td>-</td>
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</tbody>
</table>

Figure 4: Average monthly air temperature recorded on site at the Zumwalt Weather Station (ZUMWX) and downloaded from the PRISM dataset.
Figure 5: Average monthly cumulative precipitation recorded on site at the Zumwalt Weather Station (ZUMWX) and downloaded from the PRISM dataset.

Figure 6: Average monthly vapor pressure deficit recorded on site at the Zumwalt Weather Station (ZUMWX) and downloaded from the PRISM dataset.
**Seasonal Trends in Soil Moisture, Drought Stress and Vapor Pressure Deficit**

Across the sampling period from May through September, riparian aspen stands showed significantly higher season long mean average soil moisture in the 0 – 40 cm horizon in comparison to upland stands (one-way Anova, $F_{2,27} = 14.8$, $P < 0.001$). Riparian stands had an average of 5.6% cm$^3$/cm$^3$ VWC higher (95% CI: 2.9 to 8.3) than uplandSnow stands, and 5.3% cm$^3$/cm$^3$ VWC higher than other upland stands (95% CI: 2.6 to 7.9) (lsmeans linear contrasts). There was no evidence of a difference in season long mean average soil moisture in the 0 – 40 cm horizon between upland and uplandSnow habitat types (one-way Anova, $F_{1,23} = 0.30$, $P = 0.59$). Across all aspen stands, soil moisture in the upper 40 cm of the soil surface declined throughout the sampling period, consistent with the dry summers typical of this region (Figure 7). Variability across measured stands was relatively constant through the study period. The steepest decline occurred between June and July as spring precipitation ceased, yet soils continued drying, albeit less abruptly, through the September sampling period. As expected, riparian stands had generally higher soil moisture compared to both upland stand types; this difference was especially apparent during the summer months as soil moisture retention remained higher in riparian areas (Figure 7).
Figure 7: Average monthly soil moisture in the 0 – 40 cm soil horizon measured across 30 aspen stands on the Zumwalt Prairie Preserve. Bold lines indicate median values, upper and lower box ends indicate upper and lower quartiles, dots indicate stand averages that are greater or less than three times the interquartile range.

Data collected from the soil moisture station demonstrated this same pattern of soil moisture decline between June and July (Figure 8). These continuous measurements also demonstrate a lack of detectable increased moisture during the summer season until October when fall precipitation returned to the prairie. Data collected for 2018 was available for this analysis through August 8th and demonstrates high fidelity to previous measurements taken during the 2017 study period (within .01 – 2.6 cm³/cm³ VWC based on comparisons between each of the six probes on July 1st and August 1st). This suggests that soil moisture trends observed in the study area during 2017 may hold true for 2018 (Figure 8).
Figure 8: Average daily soil moisture values at 40 and 70 cm depths measured by the soil moisture station in aspen stand 1 on the Zumwalt Prairie Preserve.

Hourly vapor pressure deficit increased from the May through the July study periods where it reached its season peak before declining in August and September (Figure 9). Variability in hourly vapor pressure deficit increased throughout the summer season, demonstrating large fluctuations during the September sampling period, driven by larger swings in daily temperature and humidity (Table 4). Since weather data was not collected in each stand, patterns in vapor pressure deficit differences between stand types shown in Figure 9 can only be attributed to random chance, potentially contributing to a significant source of variation in drought stress (Figure 10).
Figure 9: Average hourly vapor pressure deficit recorded on site at the Zumwalt Weather Station. Bold lines indicate median values, upper and lower box ends indicate upper and lower quartiles, dots indicate stand averages that are greater or less than three times the interquartile range.

There was no evidence of a significant difference in summer season mean average midday xylem water potential between aspen habitat types (one-way Anova, F_{2,27} = 0.52, P = 0.60). Across the sampling period, mean average midday xylem water potential decreased from the May through July sampling periods where it reached its most negative values (highest drought stress) for the season before declining in August and September (Figure 10). Rather than following trends in soil moisture as expected, this pattern roughly followed trends in hourly vapor pressure deficit (Figure 10). This is also true of variability in summer season midday water potential measurements, which increased from the July through the September sampling periods (Table 4). This suggests that midday drought stress may have been driven by atmospheric conditions in addition to soil moisture limitation during the sampling period.
Figure 10: Stand average midday stem xylem water potential measured across 16 aspen stands on the Zumwalt Prairie Preserve. Bold lines indicate median values, upper and lower box ends indicate upper and lower quartiles, dots indicate stand averages that are greater or less than three times the interquartile range.

There was no evidence of a significant difference in summer season mean average predawn xylem water potential between aspen habitat types (one-way Anova, $F_{2,27} = 0.25$, $P = 0.10$). Predawn xylem water potential was anomalously high in May for all habitat types (Figure 11). This is unintuitive considering that soil moisture content was highest during this sampling period and both air temperatures and vpd were at their lowest relative to other sampling months. Leaves sampled during this period were not fully flushed in many cases, potentially explaining these high values. In any case, May and June xylem water potential measurements were not used in mixed model analysis due to lack of ecological significance of spring drought stress. Predawn xylem water potential followed expected patterns from June through September, steadily
decreasing across habitat types (Figure 11). Variability in predawn water potential was relatively consistent across sampling periods until September where it was much higher (following patterns in midday water potential and vapor pressure deficit) (Table 5).

Figure 11: Stand average predawn stem xylem water potential measured across 16 aspen stands on the Zumwalt Prairie Preserve. Bold lines indicate median values, upper and lower box ends indicate upper and lower quartiles, dots indicate stand averages that are greater or less than three times the interquartile range.

Table 5: Seasonal trends in water potential, soil moisture and vapor pressure deficit. Sampling period means across all 16 focal stands. Water potential measurements are averaged across all height classes. Soil moisture values are averaged across all soil depths. Hourly vapor pressure deficit is calculated for midday sampling hours from weather data recorded at the Zumwalt Prairie Preserve Weather Station.

<table>
<thead>
<tr>
<th>Sampling Period</th>
<th>Predawn Xylem Water Potential (mPa)</th>
<th>Midday Xylem Water Potential (mPa)</th>
<th>0 – 40 cm Soil Moisture (cm²/cm²)</th>
<th>Hourly Vapor Pressure Deficit (kPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± SD</td>
<td>Mean ± SD</td>
<td>Mean ± SD</td>
<td>Mean ± SD</td>
</tr>
<tr>
<td>May</td>
<td>-0.45 ± 0.08</td>
<td>-0.87 ± 0.21</td>
<td>34.78 ± 3.54</td>
<td>1.00 ± 0.55</td>
</tr>
<tr>
<td>June</td>
<td>-0.32 ± 0.13</td>
<td>-1.16 ± 0.20</td>
<td>27.46 ± 3.01</td>
<td>1.39 ± 0.22</td>
</tr>
<tr>
<td>July</td>
<td>-0.43 ± 0.10</td>
<td>-1.69 ± 0.30</td>
<td>9.49 ± 2.75</td>
<td>2.30 ± 0.40</td>
</tr>
<tr>
<td>Aug</td>
<td>-0.54 ± 0.13</td>
<td>-1.51 ± 0.25</td>
<td>7.94 ± 2.67</td>
<td>2.11 ± 0.61</td>
</tr>
<tr>
<td>Sept</td>
<td>-0.63 ± 0.19</td>
<td>-1.43 ± 0.38</td>
<td>7.04 ± 2.21</td>
<td>1.79 ± 1.04</td>
</tr>
</tbody>
</table>
Upland Soil Moisture Modeling

No interactions between predictor variables were found for upland soil moisture models. The final SmSpring model dropped all predictor variables with the exception of the categorical variables Depth and Topo (Tables 1 and 6). The final SmSummer model included Depth, Topo and both planform and profile curvature (Tables 1 and 6). All soil moisture estimates for the SmSummer model reported below were generated while holding both curvature variables at their means. Aspect was included in some top SmSpring and SmSummer models but was dropped as it was statistically insignificant and its inclusion did not improve model fit.

Table 6: Generalized least squares model results for SmSpring (May through June average soil moisture) and SmSummer (July through September average soil moisture). Variables are described in detail in Table 1.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>SmSpring</th>
<th>SmSummer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coefficient</td>
<td>T-value</td>
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<td>(Intercept)</td>
<td>28.0</td>
<td>48.72</td>
</tr>
<tr>
<td>Depth</td>
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</tr>
<tr>
<td>TopoUplandSnow</td>
<td>1.7</td>
<td>2.68</td>
</tr>
<tr>
<td>Planform Curvature</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Profile Curvature</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

During the late spring, May through June sampling rounds, upland habitat types had a mean average soil moisture value of 29.9% cm³/cm³ VWC in the 0 – 40 cm soil horizon (95% CI: 29.3 to 30.6). By the summer, July through September sampling rounds, mean average soil
moisture had fallen to 6.2% cm$^3$/cm$^3$ across upland aspen stands (95% CI: 5.8 to 6.5) (Table 6). Across upland aspen stands, May through June soil moisture was 6.9% higher in the lower 20 - 40 cm soil horizon than in the 0 - 20 cm soil horizon (97.5% CI: 2.3 to 11.9%). During the summer season, there was much more variability between 0 - 20 and 20 - 40 cm soil horizons with lower depths having a 14% higher mean average volumetric water content (97.5% CI: 1.0 - 29%) (Table 6). Perhaps more interestingly, during late spring, uplandSnow habitats had an average of 5.4% higher soil moisture than other upland habitats throughout the 0 – 40 cm soil horizon (97.5% CI: 1.0 to 10.0%) (Figure 12). The data suggests an inversion of this difference by summer with uplandSnow habitats having lower average soil moisture in the 0 – 40 cm horizon ($F_{1,45} = 4.3$, $P= 0.04$). However, when a pairwise comparison is made and correctly adjusted for multiple comparisons, there appears to be no significant difference in summer soil moisture between upland habitat types (97.5% CI: -1.0 to 28%) (Figure 12). These results should be interpreted with caution as statistical comparisons between separate model results are not possible, yet they do indicate potentially changing upland soil moisture dynamics as the season progresses.
Of all topographical variables included in initial models, only profile and planform curvature were significantly associated with soil moisture (Table 6). Profile curvature is the relative concavity of a landform perpendicular to hillslope, with positive values indicating more concave features. Profile curvature in upland aspen stands across the ZPP ranges from -0.29 to 0.88 (Table 2). Planform curvature is the relative concavity of a landform parallel to hillslope, with negative values indicating more concave features. Planform curvature in upland aspen stands across the ZPP ranges from -0.51 to 1.08 (Table 2). From July through September, across all upland stands, while accounting for soil moisture depth, an increase in profile curvature of 1 unit (higher concavity parallel to slope) was associated with a 50% increase in mean average 0 - 40 cm soil moisture (95% CI: 31– 66%), and a decrease in planform curvature of 1 unit (higher
concavity perpendicular to slope) was associated with a 49% increase in mean average 0 – 40 cm soil moisture (95% CI: 35 – 61%) (Table 6, Figure 13).

Figure 13: Associations between topographical curvature and mean average summer soil moisture (% volumetric water content). A: Planform curvature (lower values represent more concave surfaces perpendicular to slope). B: Profile curvature (higher values represent more concave surfaces parallel to slope).

**Drought Stress Modelling**

During the summer season, juvenile and mature aspen exhibited 0.38 lower mean average midday xylem water potential compared to sucker aspen (paired t-test, $t_{41} = 6.3$, 95% CI: 0.24 to 0.52). No significant interactions between predictor variables were found for summer season midday drought stress models. Of the many predictor variables selected for initial models, all final midday models included only four predictors each, three of which were shared between each model: Month, SM$_{av}$ and VPDh (Tables 1 and 7).
Table 7: Linear mixed model results for summer midday (July through September) drought stress models. Variables are described in detail in Table 1.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>MDs Coefficient</th>
<th>t-value</th>
<th>p-value</th>
<th>MDt Coefficient</th>
<th>t-value</th>
<th>p-value</th>
<th>MDav Coefficient</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
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<td>0.000</td>
<td>1.80</td>
<td>7.19</td>
<td>0.000</td>
<td>1.57</td>
<td>7.44</td>
<td>0.000</td>
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The association between soil moisture and water potential was variable depending on height class. For values averaged across height classes, while accounting for hourly vapor pressure deficit and soil texture class, a decrease of 10% cm³/cm³ VWC was associated with a 0.39 MPa decrease in mean average stem water potential (95% CI: 0.05 to 0.72) (Table 7, Figure 14). This association was strongest for aspen suckers where a decrease of 10% cm³/cm³ VWC was associated with a 0.52 MPa decrease in mean average stem water potential (95% CI: 0.08 to 0.97). This association was inconclusive for juvenile and mature trees where we found that the relationship was not statistically significant (F_{1,24} = 3.16, P= 0.09). The association between hourly vapor pressure deficit (VPDh) and midday water potential was strong across all height class models (Table 7). For values averaged across height classes, while accounting for soil moisture and texture class, a 1 kPa increase in hourly vapor pressure deficit was associated with
a 0.19 MPa decrease in mean average stem water potential (95% CI 0.10 to 0.29). For aspen suckers, a 1 kPa increase in hourly vapor pressure deficit was associated with a 0.22 mPa decrease in mean average stem water potential (95% CI 0.10 to 0.34). For mature and juvenile aspen, a 1 kPa increase in hourly vapor pressure deficit was associated with a 0.16 MPa decrease in mean average stem water potential (95% CI 0.05 to 0.26).

Figure 14: Midday water potential against average soil moisture (% volumetric water content) in the 0 – 40 cm horizon for two models. A: Sucker height class. B: All height classes averaged.
A relationship between soil texture class (TCL) and midday drought stress was evident for mature and juvenile trees and for values averaged across height classes (Table 7). While accounting for soil moisture and hourly vapor pressure deficit, for values averaged across height classes, stands with a clay loam texture class were associated with a 0.21 higher mean average midday water potential compared to silty clay loam textures (95% CI: 0.02 to 0.40). This association was stronger in mature and juvenile height classes, where stands with a clay loam texture class were associated with a mean average midday water potential of 0.29 higher compared to silty clay loam (95% CI: 0.06 to 0.53) (Figure 16). TCL was dropped from the final model for the sucker height class. Aspect was included in this model as it improved model fit yet was not found to have a significant association with mean average midday water potential ($F_{1, 14} = 2.84, P = 0.11$) (Table 7).
During the summer season, juvenile and mature aspen exhibited 0.16 MPa lower mean average predawn xylem water potential compared to sucker aspen (paired t-test, $t_{39} = 7.9$, 95% CI: 0.11 to 0.20). No interactions between predictor variables were included in final summer season predawn drought stress models. Of the many topographical and soil characteristics included as predictor variables during model selection, none of these were included in final predawn models in part due to multicollinearity issues. In comparison to other depths, soil moisture in the 0 – 20 cm soil horizon produced the best fit for the three height classes and was included in all models. Month was included as a categorical predictor in all models to allow for separate intercepts for July, August and September (Table 1). All models also included daily vapor pressure deficit from the day preceding water potential sampling (VPD1).
Table 8: Linear mixed model results for summer predawn (July through September) drought stress models. Variables are described in detail in Table 1.

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<th>p-value</th>
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<th>t-value</th>
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<td>0.17</td>
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</table>

The association between soil moisture and summer season predawn water potential varied among models for each height class (Table 8). Across aspen height classes, while accounting for Month and VPD1, a decrease of 0–20 cm soil horizon mean average VWC of 10% cm²/cm² was associated with a 0.16 MPa decrease in mean average stem water potential (95% CI: 0.07 to 0.25) (Table 8, Figure 17). This association was strongest for juvenile and mature aspen where a decrease of 10% cm²/cm² VWC was associated with a 0.21 MPa decrease in mean average stem water potential (95% CI: 0.10 to 0.31) (Table 8, Figure 17). This association was inconclusive for aspen suckers where we found that the relationship was not statistically significant (F₁,₂₆ = 0.49, P= 0.49). An association between the previous day’s vapor pressure deficit (VPD1) and predawn water potential was present in all models (Table 8). Across height classes, while accounting for soil moisture and sampling month, a 1 kPa increase in VPD1 was associated with a 0.17 MPa decrease in mean average stem water potential (95% CI 0.10 to 0.24) (Table 8, Figure 18). For aspen suckers, a 1 kPa increase in VPD1 was associated with a 0.17
MPa decrease in mean average stem water potential (95% CI 0.05 to 0.30) (Table 8, Figure 18).

For mature aspen, a 1 kPa increase in VPD1 was associated with a 0.10 MPa decrease in mean average stem water potential (95% CI 0.02 to 0.17) (Table 8, Figure 18).

Figure 17: Predawn water potential against 0 – 20 cm soil moisture (% volumetric water content) for two models. A: Mature and juvenile height class. B: All height classes averaged.

Figure 18: Mean average predawn water potential against previous day average vapor pressure deficit for three models. A: Sucker height class. B: Mature and juvenile height class. C: All height classes averaged.
Discussion

We present an analysis of aspen habitat, soil moisture dynamics and drought stress in aspen stands near the xeric fringe of aspen’s range. The 36 cm of annual precipitation received on the Zumwalt Prairie Preserve falls short of the 41 cm commonly required for aspen persistence (DeByle and Winokur 1985). This helps to explain why ZPP aspen stands are only found in either riparian areas or pockets of late season snow accumulation where soil moisture subsidies and greater soil depths may provide the necessary requirements for aspen growth. The association between late season snow cover and aspen stands was strong in comparison to the larger study area (Figure 3). This was especially true of stands at higher elevations and more northerly aspects, most of which fell into the category of uplandSnow based on their high average percent snow cover (Table 2). The fact that among upland stands those with stronger association with snow cover had higher mean average soil moisture during the spring season was intuitive (Figure 12). However, the fact that there was no difference between these stands types by summer indicates that snow cover may not be augmenting soil moisture in the 0 – 40 cm soil horizon when soil moisture is most limiting (Figure 12). It may be that differences in stand characteristics are influencing this dynamic as well. Observations of uplandSnow stands indicate that these stands generally have much thinner aspen canopies and less shrub cover compared to other upland stands. This condition could permit higher direct irradiance and local vapor pressure deficit, potentially drying soils earlier in the season compared to stands with more canopy shading. Why uplandSnow stands appear to have less aspen cover in the first place cannot be explained by ungulate exclosure status, as over half of these stands have been fully exclosed (Table A.1, appendix A). Given declining late season snow water equivalent in this region
(Mote et al. 2005), it is possible that the observed thinner density in these stands is a result of historical snow dependence and we are witnessing a positive feedback response between stand density and soil moisture (Worrall et al. 2015). Without reliable monitoring data on stand density, however, these suggestions are largely speculative, yet this could present an area of future research.

Another important limitation in discussions of late season snow cover is that cover does not account for snow water equivalent or snow depth. These attributes may be more important in associating snow to soil moisture contributions, especially in areas of heavy drifting where snow can accumulate at disproportionate depths (Soderquist et al. 2018). While analyzing late season snow cover likely accounted for snow drifts in some areas where they persisted longer into the spring season, it may have underestimated the importance of snow in some stands that accumulate heavier snow drifts. Furthermore, our model did not account for the moisture contributions of late season snow cover by adjacent topographical features. This may have underestimated the importance of snow in stands where larger areas of topographical convergence could have supplemented soil moisture resources through subsurface lateral flow. Both of these facts potentially lend further evidence to the likelihood that our snow cover model is conservative in its estimates of the association between snow cover and aspen stands; likely drifting dynamics and larger patterns of convergence further augment favorable moisture conditions for aspen growth in these upland habitats.

Summer soil moisture in both upland habitat types demonstrated strong associations with both planform and profile curvature (Figure 13). Both attributes have been shown to influence snow accumulation and drifting dynamics, with more concave surfaces capturing and retaining
more snow than convex surfaces (Lapen et al. 1996). Additionally, curvature influences surface and subsurface flow dynamics by affecting acceleration/deceleration and convergence/divergence of flow (Bogaart & Troch 2006). Surfaces that have more concave planform curvature will tend to have accelerating flow toward the steeper, backslope position of a landform and deceleration and moisture accumulation at the flatter, toeslope portion of a landform. Surfaces with more concave profile curvature will increase flow convergence, thereby increasing moisture and discharge (Bogaart & Troch 2006). Our findings of higher late season soil moisture in aspen stands of more convex surface characteristics suggest these hydrologic dynamics may be at present in upland stands.

Topographical convergence has also been associated with decreased crown mortality in areas affected by drought induced aspen decline (Tai et al. 2017). However, our analysis of both midday and predawn xylem water potential did not detect the influence of these attributes on drought stress on the Zumwalt Prairie Preserve, as curvature variables were dropped from all drought stress models (Table 1). It is important to note that this was the case of all topographical variables (with the exception of Aspect in the midday sucker models), and continuous edaphic variables, most of which were removed from drought stress models due to high multicollinearity prior to stepwise model selection (Table 1). Multicollinearity presents a significant challenge to ecological research as it is often the case that environmental predictor variables share substantial information with one another (Dormann et al. 2013).

While these variables did not prove to be significant in drought stress modelling, previous work has shown aspect, elevation, slope and curvature to be associated with aspen drought stress and drought-induced mortality (Huang & Anderegg 2012; Worrall et al. 2008, 2015; Tai et al.
2017). While attributes such as aspect, topo and soil texture class were distributed in a fairly balanced fashion across the 16 stands chosen for water potential sampling, attributes such as elevation, slope, curvature and individual elements of soil composition were considerably more heterogeneous (Table 2, Table 3). Given our inability to control for these covariates, due to small sample size and multicollinearity issues between variables, it is plausible that heterogeneity in these attributes was responsible for introducing variability into our measurements of drought stress.

This heterogeneity may have also contributed to our inability to detect differences in drought stress between aspen habitat types. While our three aspen habitat types share similarities in some attributes (e.g. riparian stands had lower slope angles, uplandSnow stands were found at higher elevations on more northern aspects) substantial variation was present in edaphic characteristics and topographical attributes such as curvature and slope (Tables 2 and 3). Despite differences in seasonal soil moisture and late season snow cover between aspen habitat types, Topo was removed from all drought stress models and we did not detect a statistically significant difference in either midday or predawn xylem water potential between habitat types (Table 1).

While we did not detect differences in drought stress in association with topographical drivers of summer soil moisture, we did find moderate evidence to suggest that soil moisture was influencing midday drought stress in our subset of aspen stands on the Zumwalt Prairie during the summer of 2017 (Figure 14). This association was strongest in the sucker height class model, somewhat weaker in the model averaging across height classes and insignificant in the juvenile and mature height class model (Table 7). The pattern observed in the average and sucker height class models of higher mean average midday xylem water potential in association with lower
mean average 0 - 40cm VWC, is consistent with published findings of aspen physiological
response to drought conditions (Galvez et al. 2011; Lu et al. 2010). Under soil moisture
limitation, xylem water potential becomes increasingly more negative throughout the plant.
Eventually these tensions become negative enough to cause air to enter the xylem through pores
in the membrane leading to cavitation (Sperry et al. 1988). Cavitation of air into the xylem can
lead to loss of hydraulic conductivity thereby restricting water transport, reducing growth and if
severe enough, leading to tissue desiccation and plant mortality (Mcdowell et al. 2013). A 50%
loss of hydraulic conductivity has been linked to global patterns of tree mortality (Anderegg et
al. 2016) and defoliation of aspen suckers (Lu et al. 2010). Published thresholds of xylem water
potential at 50% loss of hydraulic conductivity in aspen range from -2.3 to -2.5 MPa for healthy
ramets, to -1.0 MPa for ramets which had experienced previous acute drought stress; (Hacke et
al. 2001; Anderegg 2013b) and from -1.4 to -1.9 MPa in high elevation aspen to -2.4 to -2.8 MPa
in low elevation aspen (Anderegg and Hillerislambers 2016). The majority of our summer stand
level averages for midday xylem water potential fell within this range of values (Figure 10). Yet
without measurements of hydraulic conductivity or prior knowledge of the drought history of our
study stands, given this wide range of biologically significant thresholds in xylem water
potential, we cannot directly say whether these ramets were experiencing physiological damage
as a consequence of high water potentials. However, given what we know of the potential
consequences of high xylem water potential on growth, regeneration and mortality, it is still
useful to explore these patterns in the context of their underlying drivers.

The association we observed between shallow (0 – 40cm) soil moisture and drought
stress in sucker and averaged height class aspen is consistent with observations of reliance on
shallow soil moisture reserves in aspen during simulated drought stress (Anderegg et al. 2013a). Under severe moisture limitation this dependence may render aspen vulnerable to cavitation and loss of hydraulic conductance. In the case of suckering aspen this be especially true in light of the impacts of acute drought stress on loss of hydraulic conductance in aspen roots (Anderegg et al. 2012). The vast majority of aspen suckers initiate from lateral roots within upper soil surface horizons (Schier & Campbell 1978; Wolken et al. 2010). Damage to these shallow root systems, as has been observed in cases of sudden aspen decline (Anderegg 2012; Worrall et al. 2010) may be responsible for some of the patterns of weak suckering response observed following drought-induced mortality (Worrall et al. 2010). The pattern of increased midday xylem water potential in association with lower soil moisture, that we observed in our study, has also been shown to arrest growth and lead to leaf defoliation in aspen suckers (Galvez et al. 2011; Lu et al. 2010). While aspen suckers have been shown to recover after complete defoliation upon rewatering (Lu et al. 2010), cessation and reduction of growth as a result of repeated drought stress may have severe implications for long term stand health and escape from herbivory.

The fact that we did not detect a significant association between drought stress and shallow soil moisture in mature and juvenile aspen could have been due to many factors. One explanation is that the large height variability in our juvenile and mature aspen subjects was not controlled for. Tree height may exert considerable influence over water potential measurements as a result of the effects of gravimetric water potential (Lambers et al. 2008). Another explanation could be that the taller aspen are more functionally connected to deeper soil moisture reserves than the suckers in our study, considering that mature aspen have been found to have sinker roots as deep as 2.1 m contributing to soil moisture reductions (Mital and Sucoff 1983).
Considering the association between soil texture class and drought stress in our juvenile and mature aspen model, it may also be that at equivalent soil moisture levels, moisture stress in mature and juvenile ramets of our study sample is overshadowed by the influence of soil texture. It is well established that soil texture holds considerable influence over the amount of water available for plant uptake by influencing porosity (Hacke et al. 2000; Sperry & Hacke 2002). Compared to more coarsely textured soils, finer textured soils require decreased root and stem water potentials, therefore higher drought levels of drought stress, in order to extract soil moisture. This results in localized adaptations of plants to soil texture whereby plants experience differing levels of vulnerability to cavitation under equivalent levels of drought stress (Hacke et al. 2000). Experimental evidence of aspen grown in two different soil mediums has demonstrated that aspen experience cessation of leaf growth, lowered transpiration and reduced photosynthesis rates at higher soil moisture levels in finer textured soils (Lu et al. 2010). In our study, after controlling for soil moisture and vapor pressure deficit, finer textured silty clay loam soils were associated with higher mean average midday xylem water potential in juvenile and mature ramets and across averaged height classes, in comparison to clay loam soils (Figure 16). According to patterns of plant drought adaptation to soil texture, stands found in the finer silty clay loam soils may very well exhibit greater resistance to cavitation (Hacke et al. 2000; Sperry and Hacke 2002). This finding underscores the importance of considering soil physical properties in investigations of moisture stress in plant species.

Interestingly, we only found weak to moderate evidence of an association between mean average summer soil moisture and mean average predawn xylem water potential in our subset of 16 aspen stands on the ZPP (Table 8). This is despite strong associations between root zone soil
water status, or static moisture stress, and predawn xylem water potential found elsewhere (Williams and Araujo 2002). Additionally, our shallowest soil moisture measurements, (0 - 20cm) proved to produce a stronger model fit compared to 20 – 40 cm or 0 – 40 cm soil moisture, suggesting that predawn water potential is not simply reflecting water status at greater soil depths than those measured in our study. A strong association between predawn water potential and soil moisture would indicate xylem tensions in measured aspen ramets are coming into equilibrium with soil tensions as conductance ceases throughout nighttime hours (Lambers et al. 2008). The fact that we did not find this association could indicate a number of contributing factors. One explanation could be that the duration of nighttime hours in summer is insufficient to allow for xylem tensions to increase to equilibrium levels with soil in the root zone (Sellin et al. 1999). We did not test this hypothesis, but the fact that dark hour length generally tracks the pattern of observed monthly predawn water potential (in an inverse relationship) (Figure 11) warrants further instigation. Another potential explanation is that predawn water potential in our study aspen is being influenced by atmospheric conditions rather than by soil moisture status alone. This has been observed in other shrub and tree species where predawn water potential was significantly correlated to air temperature, relative humidity and vapor pressure deficit (Sellin et al. 1999). This pattern was evident in our analysis as well, indicated by a moderate but consistent relationship between average vapor pressure deficit as measured during the previous day and predawn stem water potential (Figure 18). This association was evident across all height class models unlike the association between soil moisture and predawn water potential, which was insignificant for the sucker height class (Table 8). Physiologically, this pattern of a decoupled relationship between predawn water potential
and soil moisture is in line with recent evidence of high nighttime stomatal conductance in aspen, even under drought conditions (Cirelli et al. 2015). Experimental evidence suggests that aspen may use up to 10% of its daily water budget during nighttime conductance, raising serious questions about the reliability of assuming static moisture stress conditions and plant-soil equilibrium during predawn hours (Cirelli et al. 2015).

The association between vapor pressure deficit and both midday and predawn xylem water potential highlights the importance of summer atmospheric conditions in driving drought stress in aspen. The sensitivity to aspen physiological drought response to vapor pressure deficit was the strongest and most consistent association across all of our drought stress models. Mean average midday stem water potential showed a moderate relationship with mean average hourly vapor pressure deficit across all height classes (Figure 15). The sensitivity of important physiological processes in aspen to changes in vapor pressure deficit has been well documented (Hogg and Hurdle 1997, Greer et al. 2017) and vapor pressure deficit has been linked to declining forest health and reductions in tree growth as an important driver of drought stress (Eamus et al. 2013, Restaino et al. 2016). For isohydric species such as aspen, increased vapor pressure deficit is closely related to increased transpiration rates and consequently water loss (Hogg and Hurdle 2007). Changes in vapor pressure deficit are tightly linked to changes in air temperature and concomitant changes in evaporative demand. Temperature driven anomalies in vapor pressure deficit are expected to increase under so called “global-change type droughts,” and are beginning to receive critical attention in regard to their potential impacts on forest health, independent of and in combination with, changes in precipitation patterns (Allen et al. 2010; Eamus et al. 2013; Williams et al. 2013). In the case of aspen, vapor pressure deficit has been
linked to drought-induced mortality during sudden aspen decline (Bell et al. 2014). While our study did not set out to directly link drought stress to aspen mortality, the sensitivity of physiological drought stress in our focal aspen stands to changes in vapor pressure deficit reveals potential vulnerabilities of aspen on this landscape to changing climate patterns.

Implications

Given projections of future warming and increased vapor pressure deficit (IPCC 2013); declining late season snow pack (Mote et al. 2005); and constrictions in aspen’s suitable climatic envelope (Worrall et al. 2013); the future of aspen persistence in marginal habitats is uncertain. Aspen decline in these habitats will undoubtedly be heterogeneous and aspen persistence influenced by site characteristics that create the conditions for hydrologic and climate refugia. Therefore, land management strategies must consider a diversity of measures along a spectrum of mitigation and adaptation according to aspen habitat vulnerability. Aspen may be especially prone to decline on landscapes where other stressors such as ungulate herbivory or conifer encroachment may further weaken stand resilience (Bartos et al., 1998; Bartos and Campbell, 2001). Therefore, land managers must search for novel solutions to confront multiple threats to resilience if mitigation and conservation is the goal.

Vulnerability or resilience may be challenging concepts to define let alone quantify. Yet an understanding of how measurable site attributes influence important hydrological or physiological processes in aspen stands can help refine these concepts at the site level. In the case of our research, revealing how topographical curvature influences summer soil moisture; and how both shallow soil moisture and soil texture influence aspen water relations may help to
prioritize conservation activities. For example, given that conifer encroachment into aspen stands may be associated with decreased water yield and altered soil properties (LaMalfa and Ryle 2008; Dobarco and Miegroet 2014), stands vulnerable to conifer encroachment with low topographical curvature or finer soil texture may warrant prioritized conservation efforts. Under this scenario, management may involve conifer reduction, which in the face of herbivory pressure may confront multiple threats if conifers are felled strategically to create ungulate deterrents (Seager et al., 2013). An understanding of the association between relative snow cover and aspen distribution, and the role of snow cover in contributing to soil moisture, may help to further target conservation in the context of ungulate herbivory pressure. Snow harvesting using drift fences has been shown to increase soil moisture and increase restoration success in arid systems (David, 2013). Integrating drift fence design into ungulate exclosure construction could serve to both reduce the damaging effects of ungulate herbivory and increase soil moisture reserves of snow dependent aspen stands.

Strategizing aspen conservation, restoration and adaptation in light of changing climate may be even more challenging. Understanding how soil moisture and vapor pressure deficit contribute to physiological drought stress, however, may provide insight into the practicality of innovative strategies such as assisted migration. Using climate modeling and evidence of local adaptation, it may be possible to anticipate the response of locally adapted aspen genotypes to changing atmospheric conditions and moisture regimes and proactively introduce more drought adapted genotypes into drought prone landscapes (Gray et al. 2011). Region wide genetic transfer may be less practical into landscapes at the margins of aspen’s habitat, yet site level transfer of aspen genotypes within a landscape may prove useful given genetic diversity across
small scales (Mock et al. 2008). This genetic heterogeneity is evident on our study site where diversity in ploidy level and genetic origin has been identified (Mock, 2015 unpublished). An understanding of site attributes (such as topographical curvature, soil texture, average snow cover and aspect) and how they may influence aspen drought stress through association with soil moisture and vapor pressure deficit may also help to identify potential suitable aspen habitat. Modelling this potential suitability using geospatial data augmented with site level measurements of vapor pressure deficit could be an area of future research.

The challenge of aspen conservation in marginal habitats is considerable given the complexity and magnitude of decline. Yet these marginal arid and semi-arid habitats may be the most critical habitats for targeted conservation given aspen’s outsized role in ecosystem function and biodiversity maintenance. Conservation of this key species should be a priority for land managers, especially in the Western US. As we further refine our understanding of site specific and landscape drivers of stress in aspen, the possibility of intelligent approaches to management may become apparent.
Bibliography


APPENDICES
Appendix A: Sampling characteristics and supplementary information

Table A.1: Aspen stand sampling characteristics across the ZPP. Shaded stands are those sampled for drought stress. Topo refers to aspen habitat type. Exclosure refers to ungulate exclosure status; Full - exclosed around the entire perimeter with a 2 m fence; Partial - exclosed around a portion of the stand with a 2 m fence; Cattle - exclosed with a 1 m fence; None - no portion exclosed.

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<td>Y</td>
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Table A.2: Soil sampling intensity for each stand. For soil moisture points, two measurements (0-20, and 20-40cm) were taken at each point and each point was repeated during each sampling month. Three depth measurements were taken at each soil depth point. Two soil cores (0 - 20 and 20 - 40 cm) were taken at each soil core point.

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<th>Soil Moisture Points</th>
<th>Soil Depth Points</th>
<th>Soil Core Points</th>
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Table A.3: Xylem water potential sampling by height class for each focal aspen stand.

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<th>Mature</th>
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</table>

Figure A.1: Mean average volumetric water content (VWC) at 0-20 cm and 0-40 cm soil depths during late spring (May-June) and summer (July-September) for two upland aspen habitat types. Error bars represent 95% confidence intervals. Note the shift in soil moisture from the late spring to summer seasons between the two habitat types.
Figure A.2: Boxplots showing the association between soil texture class and summer midday xylem water potential averaged across aspen height classes. Two soil texture classes, SiCL: silty clay loam, and Cl, clay loam. Note the lower mean average midday xylem water potential associated with the finer texture class.
Appendix B: Google Earth Engine snow cover code

Description: this code was used to generate a table of average snow cover values on the ZPP for each stand for each landsat image from March – May of 1984 – 2017. The process was repeated multiple sets of landsat 5 and 8 images in Step 2 (in order to avoid overly large processing) then the resulting tables were compiled and analyzed together for the entire 33 – year dataset.

// Importing ZPP upland boundaries
var zpup = ee.FeatureCollection('users/nearya/zppboundcomplete');
Map.addLayer(zpup, {color: 'FF0000'}, 'colored');

// Importing ZPP aspen stand boundaries
var stands = ee.FeatureCollection('users/nearya/AspenStands1');
Map.addLayer(stands, {color: 'FF0000'}, 'colored');

// Step 2
// importing the feature collection for processed NDSI landsat 8 images filtered to the
imageCollection = ee.ImageCollection("LANDSAT/LC8_L1T_8DAY_NDSI");
var landsat8= ee.ImageCollection('LANDSAT/LT5_L1T_8DAY_NDSI').filterBounds(zpup)
  .filterDate('2004-01-01', '2013-01-01')
  .filter(ee.Filter.calendarRange(3,5,'month'));

// setting a NDSI threshold for detection of snow
var snowThreshold = 0.4;
// snow function:

var snowfunction = function(image) {

    // add the NDSI band to the image
    var NDSI4 = image.select(['NDSI']);

    // get pixels above the threshold that classifies as snow
    var snow01 = NDSI4.gt(snowThreshold);

    // mask those pixels from the image, (pixels above threshold)
    image = image.updateMask(snow01).addBands(NDSI4);

    // Calculate the TOTAL area covered by snow in each image,
    var area = ee.Image.pixelArea();
    var snowArea = snow01.multiply(area).rename('snowArea');

    // adding the snow covered area band to the image
    image = image.addBands(snowArea);

    // Creating a function to iterate this snow cover calculation over multiple
    // images at a 30 m pixel scale
    var stats = snow01.reduceRegion({
        reducer: ee.Reducer.sum(),
        geometry: stands,
        scale: 30,
    });
    return image.set(stats);
};

// applying the snow function to the entire collection then printing the first
// image of the collection
var first = landsat8.map(snowfunction).first();
print(first, "first");

// applying the function to the entire landsat8ndsi collection filtered by date
// returning a collection that can then be processed
var collection = landsat8.map(snowfunction);

// reducing this collection over the stands to get stand level snowarea means
// returning a feature collection as the final element
var SnowSum = collection.map(function(img) {
  return img.reduceRegions(
    {
      collection: stands,
      reducer: ee.Reducer.sum(),
      scale: 30,
    }
  ).map(function(f) {
    return f.set('date', img.date());
  });
}).flatten();

// printing the results to visualize
print(SnowSum, "SnowSum")

// printing these values to a table
Export.table.toDrive(
  {
    collection: SnowSum,
    folder: "Snowarea results",
    selectors: ["snowArea", "Stand_ID", "date", "NDSI", "Shape_Area"]
  },
);
Appendix C: Photographs

Figure C.1: Visual evidence of aspen canopy mortality, possibly due to drought.
Figure C.2: Hydrometer soil texturing.
Figure C.3: Soil moisture station installed in aspen stand 1.