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Title: Water Use and Competitiveness of *Senecio sylvaticus* in Young *Pseudotsuga menziesii* Plantations in Western Oregon.

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Competition for soil water resources between newly planted Douglas-fir seedlings and aggressive early-seral plants, such as *Senecio sylvaticus* [L.] (Woodland groundsel, Senecio), can create drought conditions that impact tree seedling physiology, growth and likelihood of mortality. However, the specific impact of Senecio on soil moisture dynamics and inducement of water stress in newly planted tree seedlings across site conditions has not been quantified. This project quantified these interactions at three varied sites across the Pacific Northwest: the Coastal Range, the Cascade foothills, and the fringe of south-central valley. We tested whether water competition between Senecio and Douglas-fir seedlings in areas of high abundance of Senecio caused increased water stress in the tree seedlings. Overall, this study showed greater percent cover of Senecio was associated with greater soil moisture depletion. This soil moisture depletion was correlated with increased Douglas-fir water stress. There were also significant differences between and within species for biomass partitioning and phenotypic responses across the sites. The results here showed that there is a strong influence of site conditions on the degree of sensitivity of Douglas-fir to Senecio presence; the dry site saw the greatest shifts in biomass partitioning, the most observable water depletion, and the greatest amount of measured water stress.

These results can be useful for determining effective Forest Vegetation Management regimes that take into account the presence of Senecio and the likely impact of this presence on crop tree drought stress based on site conditions.

Water Use and Competitiveness of *Senecio sylvaticus* in Young *Pseudotsuga menziesii* Plantations in Western Oregon

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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.

Reed John Cowden, Author

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Introduction

Competition for soil water resources between newly planted tree seedlings and aggressive early-seral plants, such as *Senecio sylvaticus* [L.] (Woodland groundsel, Senecio), can create drought conditions that impact tree seedling physiology, growth and likelihood of mortality. Drought is the predominant world-wide environmental factor associated with mortality in the plant world (Allen et al., 2010). The intensity and duration of drought conditions, or water availability combined with temperature factors, determines the distribution of plants over the earth's surface (Kramer and Boyer, 1995). The Mediterranean climate of the Pacific Northwest (PNW) produces prolonged summer drought periods on many sites throughout the region that limits the growing season for crop trees and defines the vegetation community that can survive there (Powers and Reynolds, 1999). This drought condition can be exacerbated in newly established forest stands by Senecio-tree seedling competition for soil water, as Senecio has been observed to rapidly colonize regenerating forest plantations (West and Chilcote, 1968; Dyerness, 1973). Previous observational studies at the Vegetation Management Research Cooperative (VMRC) at Oregon State University (OSU) have also shown that plots almost exclusively colonized by Senecio had more water depletion per unit cover % than mixed vegetation communities in untreated control plots (Guevara et al., 2018 and 2019).

Water availability is one of the most important requirements for tree-seedling growth and development, as water is the main constituent of plant living cells, operates as a good solvent, and allows the movement of nutrients and carbohydrates throughout the plant, for example (Kramer and Boyer, 1995). Furthermore, a reduction in water availability and subsequent water stress reduces plant stomatal conductance and, hence, carbon fixation and growth (Khan, 1996). A long enough deficit in water may have irreversible effects on photosynthetic machinery, induce permanent enzyme failure, and damage root and shoot systems because of extreme water potentials and subsequent cavitation (Kramer and Boyer, 1995; Khan, 1996).

The presence of aggressive vegetation competition reduces a site's available water and increases the drought stress tree seedlings experience as a result of trying to utilize water that rapidly becomes trapped to soil particles in varying degrees depending on the soil type. Because of water's strong cohesive properties and the hydrophilic nature of soil particles, water in clay soils is stuck more tightly to the smaller particles than water in sandy soils with larger particles. This is because clay soils have more surface area per gram of soil (higher surface area-to-volume ratio) than sandy and silty soils (lower surface area-to-volume ratios) to which water can cohere. In order to absorb water, the plants must generate a strong enough water potential gradient from the transpiring leaves through the stem and into the roots that is low enough to overcome the matric potential of the soil; the lower the water potential, the greater the chance of cavitation or embolism in the xylem of crop trees (Kramer and Boyer, 1995).

It is of critical importance to quantify the soil water depletion by competing early seral species such as Senecio due to the reoccurring summer drought period in the PNW, abundance of Senecio across the landscape, and impacts of drought on planted seedling survival and growth. A reduction in soil water by Senecio can lead to an extension of the drought season, stomatal closure, and impacts on tree seedling growth and health by metabolically ramping down photosynthate production; this stressed state produces a feedback loop between carbon availability and hydraulic conductance potential (McDowell, 2011). This feedback also prompts fine root loss, reduced xylem transport efficiency and cavitation fatigue (Eilmann et al., 2009; Hacke et al., 2001). An improved understanding of competition dynamics between Senecio and planted tree seedings will also help to optimize vegetation control treatments, which are essential for buffering crop tree growth patterns. This is important to address, as the dynamics and the amount of soil water used by Senecio under varying site conditions is unknown in the literature. The consequences of this soil water depletion on Douglas-fir seedlings is also not well understood.

This research project investigated the degree of competitiveness of Senecio by analyzing soil moisture depletion, the inducement of drought stress, and the plant allometry of both Senecio and planted Douglas-fir seedlings. Our results show that a greater abundance of Senecio translated to faster soil moisture depletion and more negative xylem predawn and midday water potential of Douglas-fir seedlings. However, the degree of this impact differed across sites, largely as a result of the atmospheric and soil conditions; i.e. the impacts, which are multiplied by the soil's water holding capacity, were more extreme in the dry site than the wet sites. The sites conditions also produced three distinct phenotypes of Senecio. Previous studies have shown there is a specific threshold of tolerated abundance of competing vegetation, and therefore water competition, past which tree seedlings will suffer drought stress and possible xylem cavitation. Previous research at the VMRC has shown that this critical threshold of vegetation abundance is about 20% vegetation cover across weed types (Dinger et al., 2012). However, Douglas-fir is likely sensitive to Senecio presence as a result of Senecio's intense ruderal allocation features and other life history traits, including higher proportional root allocation and intense horizontal development of root area of influence.

This chapter will provide a background on PNW plantation forestry, FVM and herbicide use, competition dynamics, the life history traits of the invasive species Senecio, and the importance of quantifying vegetation community water use dynamics and their impacts on newly planted Douglas-fir stands.

Literature Review

Forestry in the Pacific Northwest

Forestry is an important natural resource management discipline whose relevance is increasing with the exponential growth of the human population, which is putting pressure across the globe on forests for fuel, timber, forage production, as well as a result of land-clearing trends for agricultural purposes (Jansen, 2014). Meeting this increasing demand requires practices that efficiently and successfully produce long-lived and healthy seedlings as part of the regeneration process. The Pacific Northwest (PNW) is a region in the western United States (U.S.) and Canada that comprises Oregon, northern California, Washington, and southwestern British Columbia. The area is renowned for its productive coniferous forests that are long-lived and have high biomass accumulation, which has important impacts on carbon sequestration and ecosystem health. This high productivity also makes the area an attractive economic center for wood production. For example, Oregon produced 5,459 million board feet, or 16.2% of total softwood lumber in the US in 2017 (OFRI). Oregon also accounted for about 28% of total U.S. plywood production, and it is also a leader in engineered wood products, such as Cross-Laminated Timber (OFRI). About 47% of the land area of Oregon is classified as forestland with about 80% of this classified as "timberland," which can productively grow commercial-grade timber (OFRI). The other 20% of this are reserves such as wilderness areas and national parks, as well as less-productive areas (OFRI). Most of Oregon's forests (64%) are held by state and federal agencies. In Oregon, the most important crop tree is Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), which accounts for approximately 70% of timber volume harvested (Simmons et al., 2016). Douglas-fir is a very adaptable species that thrives in many different environments. It does well in full sun and can survive in shade as well; its preferred habitats are moist well-drained soils. It achieves optimal growth patterns with areas that have hot summers and cold winters (Lavender and Hermann, 2014).

Forest Practice Regulations in Oregon

Every forest in Oregon is subject to regulations under the purview of the Oregon Forest Practices Act, regardless of their classified use. The PNW has a relatively long history of forest regulations going back to 1971, when Oregon passed the Oregon Forest Practices Act (OFRI). Washington and California passed their own forest practice regulations soon after. These rules are designed to regulate forest regeneration, management, and harvesting practices to ensure the protection of resources, including fish and wildlife habitat, soils, water, and air quality (OFRI). One of the most important regulations for reforestation operations dictates that newly planted sites should be ‘free to grow’ within six years after being planted within two years of harvest. This means that newly planted sites must have dominant trees that outcompete other surrounding vegetation (Rose and Haase, 2006). Complying with this rule can be challenging given the productive nature of these sites; this productivity lends itself to both desired and undesired species of vegetation. Ensuring sites have free to grow trees is important for abiding by the regulations, but also for improving growth potential for the desired crop species.

Forest Vegetation Management in the PNW

Forest vegetation management (FVM) is an essential part of forest planning operations, both commercial and otherwise, as competition between newly planted trees and early seral vegetation defines tree growth trajectories and survival likelihood (Hanson, 1999; Balandier et al., 2006; Wagner and Robinson, 2006). FVM can broadly be defined as practices that diminish the relative abundance of undesired vegetation species. This frees up site resources—light, water, nutrients, growing space, e.g.—for increased utilization by the desired species (Eyles et al., 2012).

Some examples of FVM treatments are manual slashing, physical removal, prescribed burning, and herbicide application.

Operationally, it is essential to use FVM during the first few years of seedling establishment to achieve the desired ‘age-shift’ of Douglas-fir trees, which shortens rotation by optimizing growth and biomass accumulation (Newton and Preest, 1988; Rose et al., 2006; Maguire et al., 2009; Dinger and Rose, 2010; Goracke, 2010). Rose et al. (2006) showed that Douglas-fir plots treated with herbicides had volume increases ranging from 63% to 355% after 12 years compared to controls. In support of this, Wagner and Robinson (2006) compared the growth rates of four conifers and found a volume increase ranging from 117% to 343% only five years after FVM. In general, it is considered that increased soil moisture availability, and subsequently reduced water stress, is responsible for these volume improvements. These studies show that freeing up site resources during the early establishment of Douglas-fir has long-lasting impacts by offering them an advantage over competing vegetation, increasing growth, allowing them to get over their transplant shock quicker, and achieving canopy closure sooner (Wightman et al., 2018; Flamenco et al., 2019).

Data from the Vegetation Management Research Cooperative (VMRC) at Oregon State University (OSU), as well as from other studies, has shown that weeds such as Senecio are an intense competitor and rapidly deplete soil water resources throughout the growing season (Dinger and Rose, 2009). The same authors showed that at least one pre-planting fall site preparation (FSP) or post-planting spring release (SR) herbicide application improved seedling growth, soil moisture levels, and water potential values compared with the controls. Furthermore, the authors demonstrated that three or more herbicide applications had significant improvements over one or two applications. Gonzalez-Benecke and Dinger (2018) showed that, for each reduction of 0.01

cm^3 cm^{-3} in soil moisture during mid-August, Douglas-fir seedling volume growth was reduced by 5.6% in the first, and 7.7% in the second growing season. Freeing this soil moisture until late August for crop trees through the application of FVM regimes is therefore crucial for ensuring optimal growth patterns and survival rates. For example, Dinger and Rose (2009) showed that a single pre-planting herbicide application kept soil volumetric water content values above 25% for an extra 28 days, while control plots had soil moisture values below 25% for about 80 days.

Failing to utilize FVM may result in a longer rotation length—and thus a lower return on investment—reductions in growth and survival of the trees, and continued expense for replanting or respraying sites after initial planting. Wagner (2000) describes how knowledge about specific species of competing vegetation influences FVM decisions. Although the impact of graminoid, herbaceous, shrub and hardwood presence on crop tree development has been established, the impact of Senecio has not specifically been tested (Cole and Newton, 1986; Newton and Preest, 1988; Rose et al., 1999; Balandier et al., 2006). This study addresses the gap in the literature by quantifying the impact of Senecio on soil moisture availability and crop tree-seedling drought stress. Understanding to what degree Douglas-fir tolerates competition with Senecio is essential to inform efficient and effective FVM operations, as Bassett (1996) showed that diameter growth down-regulation and cessation is dependent on soil moisture and evaporative demand. Conifers in the PNW complete their growth in early summer or late spring depending on factors such as precipitation, soil water holding capacity and atmospheric evaporative demand, all of which affects plant water stress that may prevent a second flushing (Khan, 1996). Without water as a limiting factor, growth can continue later into the growing season when other factors such as temperature and day length signal growth cessation.

Vegetation management utilizing herbicide application has key advantages over other methods—such as hand weeding, mulching or prescribed burning—in that it can be targeted to kill only competing vegetation, it is cheaper and more effective, it can be applied on steep or difficult terrain where other practices would be less effective or safe, and if done correctly, fewer overall treatments can be applied. Common herbicide treatments consist of a FSP followed by at least one year of SR treatment. However, many of the herbicides used in FSP treatments throughout the PNW do not effectively control Senecio spring emergence. Due to this, it is common for sites that received a FSP treatment but no SR treatment to be colonized by Senecio during the first growing season. This clears the sites of all other competition creating an ideal environment for Senecio invasion. Senecio is often the major competitor in these areas as a result. This is likely because Senecio is more sensitive to interspecific than intraspecific competition (West and Chicolte, 1968); the high tolerance for intraspecific competition leads to high vegetation densities, up to nearly 11 Mg ha^{-1} (Cowden et al., 2020).

Inter-Specific Competition

Competition between plants occurs when access to the supply of shared resources is limited; this competition limits growth, survival, reproduction, and changes allocation patterns, and can occur as the result of many disturbances and shifts in species composition (Balandier et al., 2006). Harvesting a mature stand creates a disturbance that engenders the first stages of secondary succession by freeing up site resources for any exploiting species (Dinger and Rose, 2009). These early seral species exist in complex arrays of varying competitiveness based on their likelihood of drawing resources away from the crop trees (Schoonmaker and McKee, 1988). Previous research has shown that the amount of competing vegetation is negatively correlated with the subsequent availability of soil water for crop trees (Zutter et al., 1986; Harrington and

Tappeiner, 1991; Dinger and Rose, 2009). Reducing available soil water also has consequences for nitrogen availability via microbial processes, leaching, and plant uptake which are dependent on moisture as well (Everard, 2010). This competition for water is increasingly important in the PNW given the annually recurring summer drought. The competing vegetation, especially herbaceous annuals, and the newly planted crop tree seedlings operate in the same general root zones, and thus overlap and compete for the same resources (Halpern et al., 1997).

Combining artificial regeneration with FVM allows for appropriate density, and therefore adequate growing space for each individual crop tree, while also controlling the amount of early seral species that attempt to exploit these newly available resources and outcompete the planted seedlings. Invasive species can alter ecosystem processes drastically by changing community composition and succession, as well as soil water and nutrient levels (D’Antonio and Vitousek, 1992; Khan 1996; Ehrenfeld et al., 2001). FVM regimes are undertaken to temporarily disrupt the successional stages of a site, allowing planted seedlings to become firmly established before competing vegetation succeeds. The levels of competing vegetation are generally controlled for the first 1-3 years after planting, past which growth and survival gains from managing vegetation are reduced (Wagner, 2000; Maguire et al., 2009). Failing to control the competing vegetation during this time results in intense competition that can negatively impact the newly planted seedlings. These seedlings are already at a disadvantage when planted, as they must recover from transplant damage, reestablish root-to-soil contact, and resume water and nutrient uptake (Khan, 1996; Dinger and Rose, 2009).

The potential growth of Douglas-fir crop trees in a site can be accomplished by making site resources available for their use. Reducing competition for these resources improves crop tree water and nutrient absorption, light interception, carbon fixation, and growth (Newton and Preest, 1988; Khan 1996; Rose et al., 2006; Maguire et al., 2009). Furthermore, Khan (1996) showed that too little soil water availability decreased and delayed bud initiation, budset, and bud development, and those crop tree seedlings that experienced 7% soil volumetric water content (VWC, cm^3 cm^{-3}) had 69% less height than those seedlings with 65% VWC. Another byproduct of increasing site productivity is the increased biomass accumulation and carbon fixation of the crop trees, as regenerating stands are carbon sinks (Gray et al., 2016). Flamenco et al. (2019) showed that repeated FVM treatments 5 years after planting resulted in highly efficient resource utilization and greater biomass stock accumulation by crop trees 11 years after the FVM treatments ended. Although survival is possible without combining the two approaches, achieving optimal health and productivity for stands is unlikely to occur on its own without FVM. These FVM decisions must be made even before planting, as the critical period 1-3 years after planting defines the pace and scale of growth and development for the stand over the entire rotation, and dictates the volume gained and time of harvest (Dinger and Rose, 2009; Wagner 2000).

Inter-specific competition metrics can generally be defined using vegetation cover, as this is a useful and practical proxy for informing FVM interventions (Catchpole and Wheeler, 1992). Although the crop tree seedlings can survive and tolerate a certain degree of competing vegetation—up to 20% in previous VMRC research, past which growth losses and mortality increases occur—this tolerance has not been established for Senecio (Dinger and Rose, 2009; Dinger et al., 2012). For example, Dinger et al. (2012) has shown that reducing competing vegetation below 20% during the first growing season improved Douglas-fir seedling stem volume by 273 cm^3 by year three. Wightman et al. (2019) also illustrated the impact of competing vegetation cover on crop tree stand volume at year 10; this study showed that significant reductions in volume begin at around 15-20% cover. Dinger and Rose (2009) showed that stem diameter growth for Douglas-firs undergoing herbicide treatments had more than double that of their counterparts in the control plots, and volume gains of greater than 355%. Their control treatment had 90% cover of varying species; the FSP plots were about 40% covered, with most of this vegetation being composed of introduced annual forbs, such as Senecio (Dinger and Rose, 2009). An ongoing study at the VMRC (Competition by Site Interactions Experiment, CoSInE) showed that there was greater water depletion in plots that received a FSP than the true controls that received no herbicide application (Guevara et al., 2018 and 2019). This was likely because of the predominant presence of Senecio at the FSP plots, which depleted the site of water faster than a diverse and dense vegetation community in the no herbicide plots. Therefore, the degree of tree-seedling tolerance for Senecio is likely less than the generalized 20% cover rule. The timing of this competition reduction is also key, as waiting a year to utilize a SR treatment could have long-term consequences for the stand's growth and development.

Not all species utilize site resources to the same degree, and Bell et al. (2000) showed that, for example, herbaceous species were 30% more competitive during the first four years of establishment when compared to woody species. The access to and utilization of soil water—one of the most important growth-limiting site resources—is different for the Douglas-fir crop trees and the competing vegetation because of species-specific allometric allocation to roots/shoots and life history traits. For example, Dinger et al. (2012) showed that 4 invasive species, *Cirsium arvense*, *Cirsium vulgare*, *Rubus ursinus* and *Senecio sylvaticus*, achieved maximum photosynthetic rates between 15 and 30 μmol CO_2 m^{-2} s^{-1} during the active growth phase of their life histories. This can be compared to Douglas-fir seedling photosynthesis rates of about 10 μmol CO_2 m^{-2} s^{-1} under optimal conditions (Manter, 2003). Senecio's maximum photosynthetic rate was about 25 μmol CO_2 m^{-2} s^{-1}, which is the second highest rate of the four species (Dinger et al., 2012). Although these photosynthetic rates slowed past mid-July for Senecio, the transpiration rates did not decline, even when soil water was reduced to 25% VWC (Dinger et al., 2012). Furthermore, the authors showed that Senecio had the highest transpiration rate of the four species, even in induced drought conditions. These high gas exchange rates contribute to Senecio's massive growth gains during the early season from April to mid-June.

Interventions must therefore be timed before these growth gains have been achieved to retain soil water at the site for crop tree use. For instance, Dinger et al. (2012) calculated that, with a theoretical density of nine plants m^{-2}, four early seral species, including Senecio, could deplete soil water from 40% to 25% VWC in 21 to 63 days. However, other field observations have observed Senecio inhabiting sites at a density of over 22 plants m^{-2} (West and Chilcote, 1968). With this density, it would only take 25 days for Senecio to deplete the VWC from 40% to 25% (Dinger et al., 2012). It is therefore of critical importance to quantify to what degree Senecio depletes sites of water resources to better understand and inform the need for intervening FVM treatments.

Senecio History and Life History

There are noted incidences of Senecio all over the world: in Africa, Finland, Germany, Japan, Hawaii, New Zealand, North America, Russia, South America, Spain, and the UK, among many other places in Western Europe (https://www.invasive.org). It is also widespread in the United States. It is most pervasive along the Pacific Coast from Northern Washington down to Central California. It has not been observed in the Central United States, although it has over the past few years begun to appear in Michigan. Senecio can inhabit mountainous areas up to about 1500 m.a.s.l. and it generally is not found in wetland areas (https://www.cdfa.ca.gov). It has been noted to avoid intense competition, as it prefers disturbed open areas and sites with poor soil. It is common on non-calcareous sandy or gravelly soils and dry heaths. Other common habitats are rocky outcrops, logged and burned areas, fields, meadows, roadsides, embankments, sand pits, and even wastelands (Palmblad, 1968). Senecio's preferred habitats are cool moist areas such as anthropogenic disturbed sites, coastal beaches, and forest edges (USDA).

Senecio is an invasive annual species that was introduced from Eurasia to the U.S. in the 1920s in Humboldt County, California **(**West and Chilcote, 1968**).** This species has adapted to short term dominance during the early stages of secondary succession and rapidly colonizes forest sites following disturbances. It has a life history which predisposes it to successfully colonize disturbed sites with ruderal allocation features such as rapid completion of its lifecycle and production of a large wind-vectored seed bank. Senecio can produce about 190,000 seeds m^{-2} which are generally wind dispersed during the dry period of the year from around July 15th to September 1st (Hanson, 1998; West and Chilcote, 1968). Senecio has no perennially persistent seed bank, as the population is only maintained by wind-dispersed seeds (Ernst and Neilssen, 1979). This has important management implications, as a FSP pre-emergent herbicide treatment will not effectively kill Senecio that will germinate at a later date. These small wind-vectored seeds also allow Senecio to become established in areas with accumulated harvest residues (West and Chilcote, 1968).

Senecio produces two cohorts: a fall over-wintering cohort, and a spring cohort (Hanson, 1998). In Oregon, it is this spring cohort which intensively colonizes reforestation sites, as most sites receive at least a FSP which would kill the over-wintering Senecio florets. The mean development time is different for each variety, as the summer plants flower more quickly and have a higher growth rate than their winter counterparts (Ernst, 1985). Some factors that limit establishment likelihood are insect presence, such as *Aulacorthum solani*, which is a predating aphid. This mostly affects the summer form, as the winter form produces more toxic compounds. Herbivory is unlikely considering the toxicity of the plant, although rabbits have been observed to predate it (Hanson, 1998). Senecio therefore offers few ecosystem services beyond habitat for sleeping deer and limited carbon sequestration, as it uses much of a site's available water, provides little or no forage because of its toxicity, and limits biodiversity by heavily colonizing sites.

Senecio intensively occupies sites during the first 1-3 years of initial introduction, then dramatically decreases its population presence past this (Hanson, 1998). It is thought this occurs because of the intensity of its adaptive life history which predisposes it to quick early successional apical dominance which depletes the soil resources needed to produce achenes of the appropriate robustness (West and Chilcote, 1968). This low fecundity over time results in a diminishing population presence. Nonetheless, because of the extreme early growth patterns during the initial 1-3 years, allowing Senecio to inhabit a site for even one growing season could have deleterious effects on crop tree growth patterns, especially in dry sites. Stressing the tree seedlings is not trivial, as early growth patterns can dictate mature stand species composition, impact the time until harvest, and influence mortality likelihood. Van Andel and Jager (1981) stated that since Senecio absorbs nutrients rapidly it may be less constrained by site productivity than other species. This may explain why Senecio can grow in many poor-quality sites that other plants cannot. There is also a noted sensitivity to organic compounds produced by broadleaves, which helps to explain its preponderance in conifer forests on the western United States Pacific Coast, as well as other coniferous forests across the world (Ernst, 1985).

Senecio is an annual composite with rayless yellow flowers that curl upwards from a single stem (Hanson, 1998). These flowers usually exist in a fan at the end of a cluster (Hanson, 1998). Its fruit are cylindrical, ridged, sparsely haired, and dark brown with an achene that is about 2.5

mm long; the tips of these achenes have hairs which aid in wind dispersal (Hanson, 1998). Interestingly, the density of the parent generation does not affect germination rates, although it does impact the integrity of the seed pods (Palmbald, 1968). The bolting rosettes can eventually achieve a height greater than one meter, and they flower during mid-June through mid-July (Hanson, 1998). These autogamous, or self-fertilizing, flowers produce an incredible number of stiffly-haired achenes that develop about 15 days after anthesis when the flower bud opens up (Pojar and MacKinnon, 1994; Ernst, 1985).

Senecio's achenes are very light which gives them a good chance to spread from one open habitat to another via wind dispersal. These achene hairs allow dispersal via animals and machinery as well, as the tufted hairs can tangle with socks, clothing, equipment, and animal hides. Senecio is also pollinated by flies, bees, and wasps, but this is not an essential part of its life cycle, as it can self-pollinate. Interestingly, the pollen from Senecio can be deposited by an insect to another species such as *Senecio viscous* and can crossbreed with it (Hanson, 1998). Senecio seeds germinate with no delay or dormancy because of their inability to protrude through the endosperm (Ernst and Nelissen, 1979; Ernst, 1985). This information reinforces the need for management regimes that control Senecio abundance over the growing period through targeted herbicide application such as SR treatments after a FSP.

Objectives and Hypothesis

The overarching goal of this research was to quantify the consequences of early seral competition by Senecio in Douglas-fir plantations and assess this impact on tree seedling physiology as a result of water depletion and subsequent water stress. This information can be used to support management decisions to effectively and efficiently control weed species, such as Senecio, that compete with crop tree production. The first objective of this project was to quantify the soil water dynamics under varying abundance of Senecio across a range of sites in Western Oregon. The second objective was to quantify the effect of Senecio abundance on Douglas-fir seedling drought stress using predawn and midday water potential assessments. The third objective was to observe differences in allometry and root architecture between and within species across sites.

This study hypothesizes that:

1) A greater abundance (cover % and height) of Senecio is correlated with increased soil moisture depletion.
2) Lower soil water availability will induce competition between Douglas-fir seedlings and Senecio which will increase water stress in Douglas-fir seedlings to varying degrees across different environments. We predict that those Douglas-fir seedlings growing with higher abundance of Senecio around them will show increased local soil water depletion, and have higher water stress (more negative predawn and midday water potential).
3) In response to limiting soil moisture, root architecture and biomass allocation will be preferentially emphasized to a greater degree in the invasive species Senecio compared to Douglas-fir.

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Chapter 2: Seasonal Dynamics of *Senecio sylvaticus* Abundance and its Effect on Soil Moisture at Three Sites in Western Oregon

Introduction

Growing crop trees efficiently—achieving low mortality and maximizing growth without large input costs—requires that site resources are allocated primarily for their uptake and use. This increasing need to grow trees faster and efficiently is the result of many different socioeconomic pressures, such as the fossil fuel crisis necessitating an interest in biofuels, the opportunity cost of competing ventures if tree plantations are not profitable enough, and the increasing population pressure for wood products, including fiber, fuel, structural material, and pulp (Parde, 1980; Jansen, 2014). Understanding how trees grow optimally is useful in many different applications from industry to research, as an accounting of Carbon fixation and water use dynamics is useful for estimating potential productivity of a site. Further optimization of reforestation efforts could be an important part of the carbon credit market in Oregon, as young forest plantations sequester carbon at a faster rate than older ones (Gray et al., 2016). Ensuring that these crop trees are free to grow by accounting for the likely impact of competing vegetation on site water balance is important from a legal standpoint (e.g. Oregon Forest Practices Act) as well as an operational one. Defining this optimization is an important question that deserves further consideration.

Water dynamics, including the Soil-Plant-Atmosphere Continuum (SPAC), are of primary importance to consider for site assessments given that this is the foundation of growth and productivity. A consideration of soil characteristics, such as bulk density, particle size distribution, water holding capacity, and seasonal precipitation dynamics informs the likely impacts of the soil and water conditions on crop tree species. Furthermore, it is important to consider how the presence or absence of competing vegetation changes the SPAC of the crop trees, as reducing available water content in the surrounding area induces drought stress and shortens their growing season (Fernandez et al., 2014). This reduction in available water and subsequent growth, if severe enough, can eventually result in cavitation and crop tree mortality (Nardini et al., 2013).

This chapter discusses the seasonal dynamics of *Senecio sylvaticus* [L.] (Woodland groundsel, Senecio) abundance and the relationship with water use and subsequent depletion in different environments. Analyses were done on soil moisture, Senecio abundance, and weather variables between and within sites to get an understanding of the variation of these relationships across geographic regions, from the Cascade foothills to the Coastal Range in Oregon. Senecio is abundant across these landscapes, and this chapter illustrates the degree of this impact, which is especially poignant in dry sites compared to wet ones.

Literature Review

Soil-Plant-Atmosphere Continuum Dynamics

The particle size distribution (i.e. percentage of sand, silt, and clay) in soil dictates key physical properties. These physical properties can be used to predict likely behavior and impacts using pedotransfer functions to determine soil hydraulic conductivity, the upper and lower limits of water retention, and available soil water, for example. The same volumetric amount of water in soils of different textural classes has vastly different availabilities and potential for exploitation by plants (Kramer and Boyer, 1995). Clay soils are composed of fine, compact, and cohesive particles that have a large surface area (30 m^2 g^{-1} of soil) which stores much water and minerals, but this comes at the cost of poor drainage and little aeration which are essential for plant growth; a lack of drainage and aeration can result in anaerobic fermentation, which is deleterious to roots (Kramer and Boyer, 1995). Sandy soils, on the other hand, are loose and non-cohesive with lots of aeration and drainage, but therefore little storage capacity and surface area (.0001 m^2 g^{-1} of soil). Silty soils have surface areas intermediate between these two ends of the particle size continuum (.1 m^2 g^{-1} of soil). One way to characterize soils regarding the degree of potential exploitation by plants is the metric of available soil water (ASW). This is the difference between the in situ field capacity, which is the water content after downward drainage has achieved equilibrium after rain, and the permanent wilting point, which is the soil water content below which plants will be wilted overnight until additional water is added (Kramer and Boyer, 1995). This is a much more valuable metric than pure soil volumetric water content (VWC, $cm^3\ cm^{-3}$), as a sandy soil may be saturated at a VWC that is the wilting point for a silty soil.

Beyond the soil-plant interface, there are also the atmospheric conditions that contribute to the likely behavior and availability of the resident site water. Temperature, for instance, affects both the driving force of the water potential gradient between the soil and roots and the resistance of water movement through the soil and roots (Kramer and Boyer, 1995). Temperature and relative humidity are the factors used for the calculation of Vapor Pressure Deficit (VPD, kPa), which is the difference between the leaf and atmospheric vapor pressures. Denmead and Shaw (1962) discussed this relationship between atmospheric conditions and soil conditions, showing that a soil water potential of -0.1 MPa was limiting when high rates of transpiration occurred, but -1 MPa was not limiting at low transpiration rates; essentially, on hot sunny days water deficits and repressed transpiration rates occurred in moist soil, but on cool cloudy days plants may not experience xylem stress in dry soil. Therefore, an amount of soil water is inadequate or adequate for a plant's needs based on the defining context of atmospheric conditions. It is therefore of critical importance to account for atmospheric conditions such as VPD and the impact of these forces on water use and growth at the different sites.

Impacts of Competition on Water Dynamics

Data from the VMRC at OSU, as well as from other studies, has shown that weeds such as Senecio are an intense competitor for and rapidly deplete soil water resources throughout the growing season (Dinger and Rose, 2009). Competition for soil water resources between newly planted tree seedlings and aggressive early-seral plants, such as Senecio, can create drought conditions that impact tree seedling physiology, growth and likelihood of mortality. The Mediterranean climate of the Pacific Northwest (PNW) produces prolonged summer drought periods on many sites throughout the region that limits the growing season for crop trees and defines the vegetation community that can survive in this region (Powers and Reynolds, 1999). This drought condition can be exacerbated in newly established forest stands by Senecio-tree seedling competition for soil water, as Senecio has been observed to rapidly colonize regenerating forest plantations (West and Chilcote, 1968; Dyerness, 1973).

Previous research has shown that the amount of competing vegetation is positively correlated with the subsequent reduction in available soil water for crop trees (Zutter et al., 1986; Harrington and Tappeiner, 1991; Dinger and Rose, 2009; Gonzalez-Benecke and Dinger, 2018). Reducing available soil water also has consequences for nitrogen availability via microbial processes, leaching, and plant uptake which are dependent on moisture as well (Everard, 2010). Competition metrics can generally be defined using vegetation cover, as this is a useful and practical proxy for approximating vegetation leaf area and abundance, and informing FVM interventions (Catchpole and Wheeler, 1992). Although the crop tree seedlings can survive and tolerate a certain degree of competing vegetation—up to 20% in previous VMRC research, past which growth losses and mortality increases occur—this crop tree tolerance has not been established for Senecio (Dinger and Rose, 2009; Dinger et al., 2012).

It is of critical importance to quantify the soil water depletion by competing early seral species such as Senecio due to the reoccurring summer drought period in the PNW, the abundance of Senecio across the landscape that can extend this drought period, and the impacts of drought on planted seedling survival and growth. A reduction in soil water by Senecio can lead to stomatal closure and impacts on growth and health by metabolically ramping down photosynthate production; this stressed state produces a feedback loop between carbon availability and hydraulic conductance potential (McDowell, 2011). This feedback also prompts fine root loss, reduced xylem transport efficiency and cavitation fatigue (Eilmann et al., 2009; Hacke et al., 2001). An improved understanding of competition dynamics between Senecio and planted tree seedlings will also help to optimize vegetation control treatments, which buffer crop tree growth patterns. Although the impact of graminoid, herbaceous, shrub and hardwood presence on crop tree development has been established, the impact of Senecio has not specifically been tested (Cole and Newton, 1986; Balandier et al., 2006; Rose et al., 1999; Newton and Preest, 1988). This study addresses this gap in the literature by quantifying the impact of Senecio on soil moisture availability.

Objectives and Hypothesis

The objective of this research project was to quantify the competitive consequences of early seral competition by Senecio across forest plantations on the availability of soil water. This information can be used to support management decisions to effectively and efficiently control competing vegetation species, such as Senecio, that compete with crop trees.

This study hypothesizes that site water depletion will increase in accordance with higher Senecio abundance values. We predict that those areas with a greater % cover of Senecio around them will show increased local soil water depletion; this will occur to a greater degree at the dry site (Veneta) compared to the other wetter sites (Sweet Home and Burnt Woods).

Methods

Site Selection

Study sites were located in newly planted Douglas-fir plantations in areas expected to have high amounts of Senecio. After consulting with VMRC cooperators, three study sites were selected in order to capture a gradient of site conditions across western Oregon. All of the selected sites received a pre-planting fall site preparation herbicide application; within each site, a uniform 0.3 ha (61 x 61 m) study area was identified and excluded from any further herbicide application. By excluding these areas from any post-planting spring release treatments, a large amount of Senecio was expected at each site.

The first site is managed by Cascade Timber Consulting Inc. and is situated on a plateau near a steep slope overlooking the town of Sweet Home (SH, Figure 1, Figure 2a). This study site is located at 44°22'00.9"N 122°42'29.7"W in the central Cascade Range of Oregon at approximately 320 m above sea level and 109 km East of the Pacific Ocean. The site has a mean annual temperature of 10.8°C, mean annual precipitation of 1705 mm, and soils in the Peavine and Kilchis-Harrington series defined as silty clay loam with stony loam (Wang et al., 2012; Soil Survey Staff, 2019). Observations also indicate that the soil has some areas that contained significant gravel and coarse material, including decomposing cedar. This site had the highest average soil clay content (36%), the lowest sand content (30%), the highest field capacity (0.39 cm^3 cm^{-3}), and lowest available soil water (ASW; 0.14 cm^3 cm^{-3}) of the three sites. This was our intermediate site, as it was neither extreme in temperature nor relative humidity. The site was planted with bareroot plug+1 Douglas-fir seedlings. The tank mix used in FSP included 2 qts. of glyphosate, 16 oz. of imazapyr, 4 oz. of Oust Extra and 8 oz. of MSO.

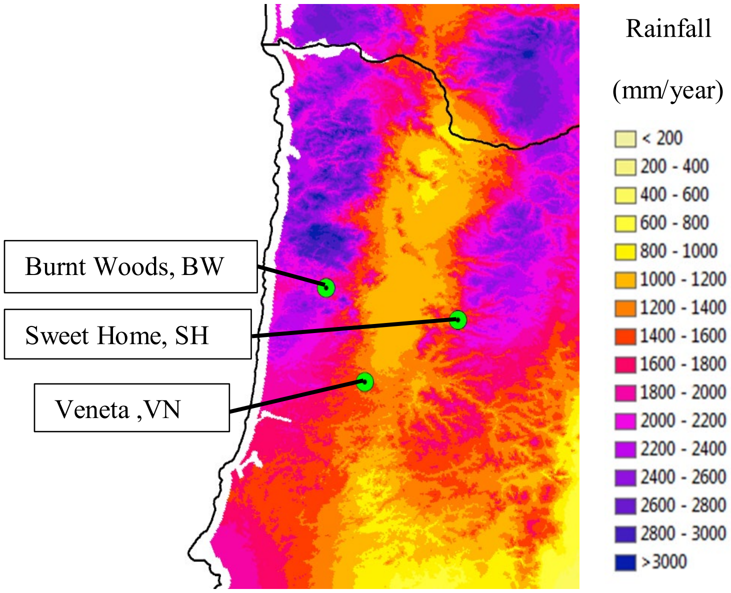

Figure 1. Location of study sites in western Oregon on a rain heat map in mm per year.

The second site is managed by the Oregon Department of Forestry and is located on a steep SE facing slope near Burnt Woods, OR (BW, Figure 1, Figure 2b). This study site is located at 44°35'14.2"N 123°40'57.0"W in the Coastal Range and is approximately 410 m above sea level and 35 km from the Pacific Ocean. The site received a broadcast prescribed burn before planting, has a mean annual temperature of 10.2°C, mean annual precipitation of 2075 mm, and soils in the Preacher-Bohannon-Slickrock complex (Wang et al., 2012; Soil Survey Staff, 2019). This soil texture consists of loam weathered from sedimentary rock types, loam from sandstone, and Slickrock gravelly loam. BW had the highest annual levels of rainfall of the three sites. This site also had the highest average soil sand percentage (36%), lowest clay content (30%), and greatest ASW (0.16 cm^3 cm^{-3}) of the three sites. The site was planted with styro 20 containerized Douglas-fir seedlings. The tank mix used in FSP included 2 qts. of glyphosate and 4 oz. of Oust Extra.

The third site is owned by Roseburg Forest Products Inc. and is located near Veneta, OR (VN, Figure 1, Figure 2c). This study site is located at 43°56'25.3"N 123°23'58.3"W in the south-central valley and is approximately 266 m above sea level and is 65 km from the Pacific Ocean. It has a mean annual temperature of 11°C, mean annual precipitation of 1422 mm, and soils in the Peavine series defined as a silty clay loam (Wang et al., 2012; Soil Survey Staff, 2019). This site had the highest average soil silt content (38%), and the lowest wilting point (0.22 cm^3 cm^{-3}). This was our dry site and it also had the most extreme weather conditions: highest temperatures, lower relative humidity (highest VPD), and the least amount of rain. The site was planted with bareroot plug+1 Douglas-fir seedlings. The tank mix used in FSP included 2.25 qts. of glyphosate 5.4, 4 oz. of Oust XP and 1 oz. of MSM 60.

Figure 2. Photos depicting MS student Reed Cowden installing the weather station at the Sweet Home (SH) site (A), a general view of the Burnt Woods (BW) site (B), and example of a clip plot at the Veneta (VN) site (C).

Soil Moisture and Weather

In order to quantify soil moisture dynamics associated with varying abundance levels of Senecio at different sites across the PNW, soil volumetric water content (VWC, cm^3 cm^{-3}) was measured using 30 cm long vertically inserted time-domain reflectometry (TDR) soil moisture sensors (CS650, Campbell Scientific, Logan, UT) during the 2019 growing season. This allows us to measure soil moisture conditions at a depth from 0 to 30 cm. At each site, a circular study area of 0.3 ha was identified with uniform terrain conditions and varying abundance of Senecio. The study area was divided into two rings: the inner ring had a radius of 21.5 m and the outer ring had a radius of 30.5 m. Both of these rings were divided into four quadrants, resulting in eight octants of equal area (Figure 3). One TDR probe was installed in each octant at a random azimuth and distance from the central point (Figure 3). By randomly selecting the location of our 8 soil moisture sensors, we expect our sensor locations represented the range of Senecio covers found across the study area at each of the sites. At the central point of the circular plot, a weather station and datalogger (CR300, Campbell Scientific, Logan UT) were installed to measure and collect all soil moisture and weather information; all data was recorded at 30-minute intervals. Weather measurements included global radiation, air temperature, relative humidity, and rainfall (Figure 2a). Given an operational spacing of 3 x 3 m, there were about 310 Douglas-fir seedlings per study area at each site.

VWC data from the TDR sensors was expressed as fractional available soil water (FASW) by analyzing the upper and lower limits of wetting and drying of the soil through the entire study period. Drained upper limits (DUL, $cm^3\ cm^{-3}$) and lower limits of water extraction (LL, $cm^3\ cm^{-3}$) were determined for each probe and FASW was calculated using the formula proposed by Ritchie (1981):

$$\mathrm{FASW} = 1 - \frac{(\mathrm{DUL} - \mathrm{VWC})}{(\mathrm{DUL} - \mathrm{LL})} \tag{1}$$

where FASW is fractional available soil water, DUL is drained upper limit, VWC is volumetric water content, and LL is the lower limit of water extraction.

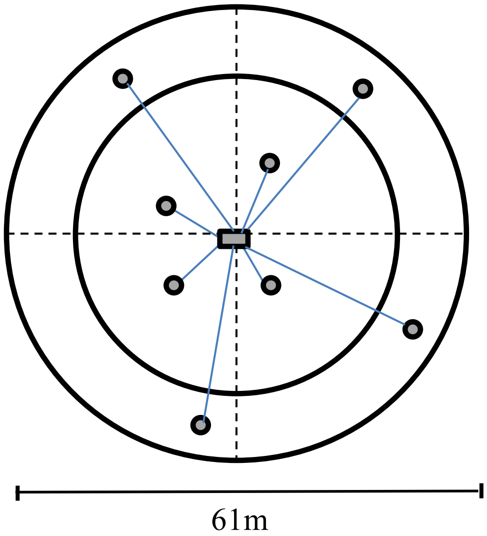

Figure 3. Diagram of sensor deployment in the study area (0.3 ha). Soil moisture sensors were deployed in two rings with the same area. The central grey rectangle represents the weather station with a datalogger. Gray circles represent the 8 soil moisture sensors.

Senecio Cover and Biomass Dynamics

Assessments of Senecio cover and height were carried out at every soil moisture probe location (n=8) at each site every two to three weeks during the growing season (between May and late September). A 1 x 1 m PVC frame was placed on the ground to measure percent cover (Figure 2c). Vegetation cover and height were estimated visually at each location. If the cover of non-Senecio species was greater than 5% in any vegetation survey area, or the areas surrounding the tree seedlings, that non-Senecio vegetation was removed by hand.

Soil Water Use by Senecio

VWC data from TDR sensors was transformed to soil water content (SWC, mm) using the inference length of the TDR sensors (i.e. 30 cm); it is assumed that changes in SWC can be used as a proxy of the water use of Senecio growing in the sensor's inference area. At each site, for each soil moisture measurement point, daily changes in SWC (or soil water depletion by Senecio) was calculated as the reduction in SWC from one day to the next. We excluded days with more than 0.1 mm rain, and the following two days. Senecio data (cover % and height measured bi-monthly) was estimated for each day at each sampling point using linear interpolation between measurement dates and was then merged with soil water use and climate data.

Statistical Analysis

Linear regression models were used to correlate Senecio cover and FASW. Sigmaplot version 14 (Systat Software, Inc. San Jose, CA, USA) was used to make all figures.

Results and Discussion

Weather Conditions

Weather stations collected data at SH and VN beginning in mid-April of 2019. Our original third site was moved in May when little to no Senecio abundance was observed; BW measurements therefore began in late May. There were differences between sites for the weekly mean weather variables from April to late September (Figure 4). The VN site had the highest temperatures, lowest relative humidity and least amount of rainfall, with little-to-no rain from June 1st until the beginning of September. The SH and BW sites both had more precipitation events, especially in June which recharged the soil and helped to reduce the length and intensity of the seasonal drought. Over the shared measurement period (5/31-9/27), the VN site had 62 mm of rain, while the SH and BW sites had 227 mm and 171 mm of rainfall, respectively. The mean growing season temperature for VN, SH and BW sites was 16.8, 16.1, and 16.2 ºC, respectively. The mean RH was 72, 75 and 81% for the VN, SH and BW sites, respectively. This data reflects that drought conditions were more intense at the VN site than the SH or BW sites.

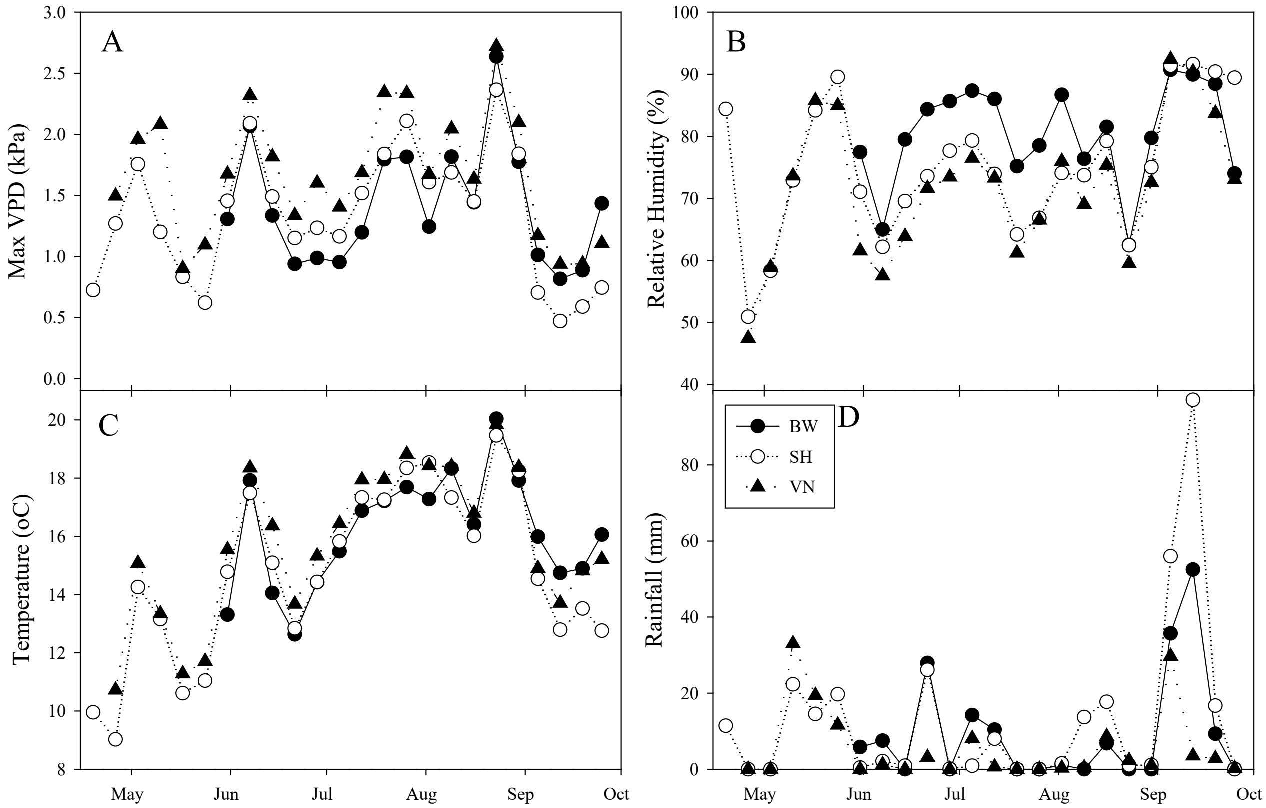

Figure 4. Weekly mean: A) maximum VPD, B) relative humidity, C) air temperature and D) total rainfall, for the BW (filled circle), SH (open circle) and VN (filled triangle) sites.

Seasonal Dynamics of Senecio Cover Percent and Height

When the sites were selected, there was little to no Senecio as they all received a FSP herbicide application. Florets were only a few centimeters wide and tall by late April. However, as the growing season progressed these florets grew rapidly and achieved heights of about 120 cm, for example at the BW site, by 6/14. Overall, the growth dynamics of Senecio during the 2019 growing season were different across the sites (Figure 5). The BW site had the tallest Senecio plants and the highest percent cover even though it had two probes with 0% Senecio cover which drove down the average (Figure 5). On the other hand, the SH site had the least cover, the shortest Senecio, but the most rainfall and the longest growing period of the three sites. Each of the sites had a general seasonal pattern of floret presence and development into apical form at around 7/15, after which senescence began to occur. The SH site was unique both in the phenotype of the Senecio, but also in the generational development; soon after 7/15 there was a second generation of summer Senecio. However, this did not occur on a large scale, with only about 4% of the 1 m^2 vegetation surveys being composed of the second generation of Senecio. This second generation did not appear at BW or VN to any degree.

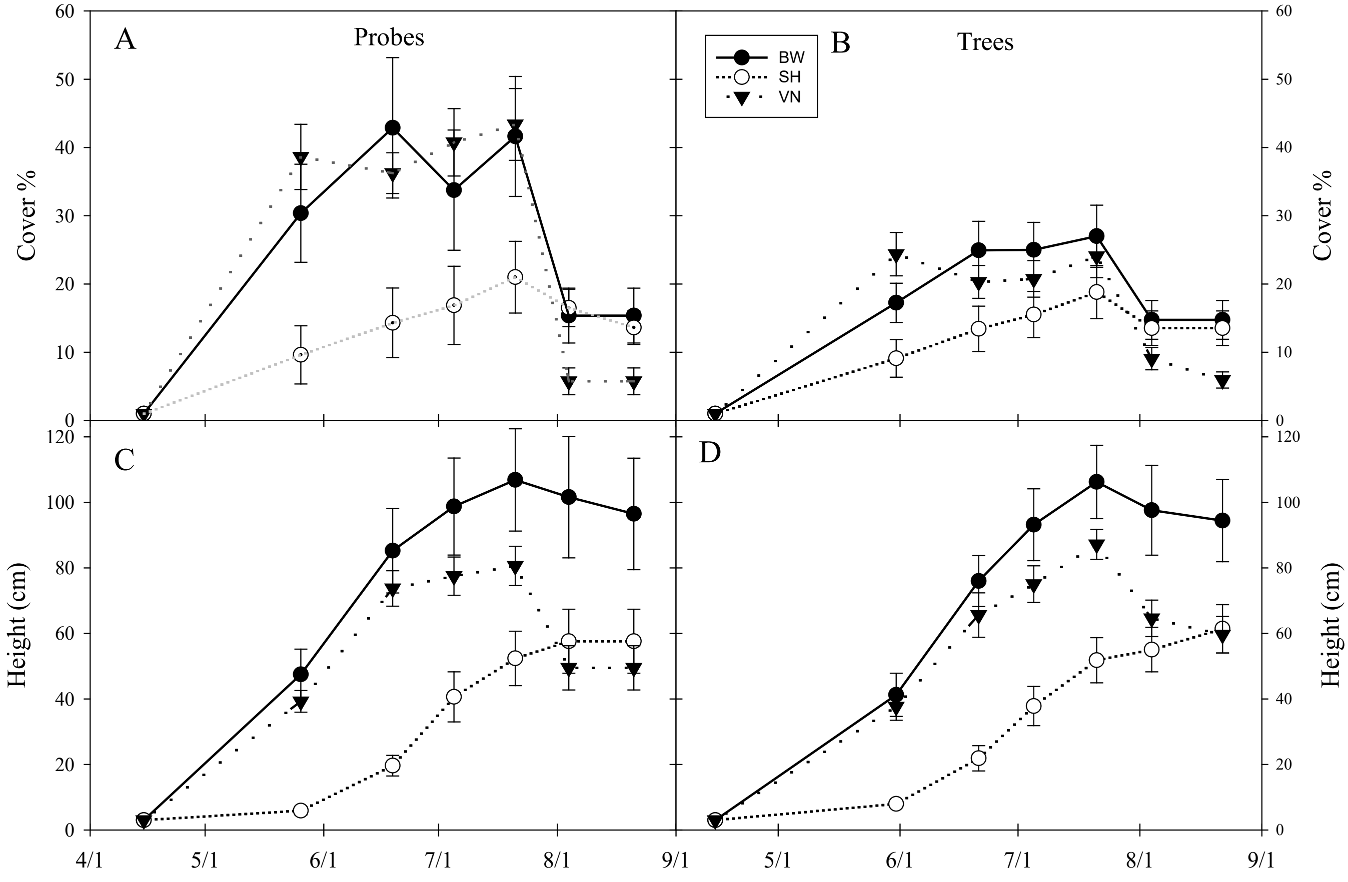

Figure 5. Seasonal dynamics of: cover percent (A, B) and total height (C, D) for Senecio growing at the BW (filled circle), SH (open circle) and VN (filled triangle) sites. Left panels show measurements taken around soil moisture probes (n=8); right panels show measurement taken around Douglas-fir seedlings (n=16).

Each site had 8 probes and 16 trees sampled (Figure 5). Within a 1 m^2 area, the trees had on average lower amounts of Senecio; this is likely because of the disturbance of the soil by the tree planter in this area. However, there were similar height levels between probes and trees. This pattern was consistent across the different sites. It is worth noting that the standard errors for the probe surveys were larger than the tree surveys because at least one probe at each site had around 0% cover.

There was a similar pattern within and between sites in the incidence of competition-induced mortality. The seasonal abundance dynamics at BW and VN, for instance, can be described as a quick early successional peak, a loss of vegetation cover— but not height—due to competition-induced mortality, and a subsequent recovery by the remaining Senecio as they expanded their florets and filled the available growing space (Figure 5). This happened earlier at the dry site (VN), and then later at the wetter site (BW); for SH, this never happened, as the abundance values never achieved those of the other two sites to induce mortality. For BW, overall a greater reduction in cover % was observed, perhaps because of intense intraspecific competition for light. For both BW and VN, the lapse was recovered up to the original values, and then they both experienced severe senescence and mortality after producing seeds between July and August; for SH, the same intense mortality and senescence did not occur. This illustrates that the degree of moisture in combination with the preponderance of other Senecio impacts site growth patterns.

To conclude, instantaneous measurements of plant traits appear to be relevant tools to predict the dynamics of species responses to resource availability under competition. This validates the use of plant traits as sensors of resource availability, particularly at the local scale at which plant–plant interactions operate, or as indicators of the effects of environmental conditions involved in the structuring of plant communities along environmental gradients (McGill et al., 2006; Shipley et al., 2006).

Soil Water Dynamics

There was a consistent pattern across the sites where FASW values were increasingly depleted as the magnitude of Senecio abundance increased (Figure 6). Maximum values of FASW (when VWC is equal to DUL) were similar among the probes at each site during the wet season, but quickly separated as the dry season progressed with probes surrounded by higher levels of Senecio having faster reduction in FASW (and, hence, faster rates of soil water depletion) (Figure 6). This is consistent with other findings, as studies have found that failing to control competing vegetation decreases soil moisture significantly compared to vegetation management regimes (e.g. Flint and Childs, 1987; Dinger and Rose, 2009). Flint and Childs (1987) also found that in SW Oregon, where water is especially limiting, Douglas-fir seedling growth patterns were diminished by competing vegetation as a direct result of water depletion; their results also showed that controlling for competing vegetation lowered soil temperature, soil evaporation, and overall water depletion.

Although Senecio abundance over the growing season was similar for the VN and BW sites (Figure 5), the impact of Senecio presence was different across sites. This was especially so at the VN site, where as a result of Senecio presence combined with more intense atmospheric conditions, the site was depleted of soil water faster and earlier than the other two sites. The VN site also experienced the most prolonged drought of the three sites, lasting for over 3 months with FASW lower than 20% in areas of high Senecio abundance (Figure 6). The impact of this depletion and subsequent prolongation of the drought period has long-term consequences both for growth (Brix, 1979) as well as nutrient availability and species composition (Everard, 2010). For instance, Everard showed that invasive annuals displaced native vegetation in dry sites in California, while wetter sites tolerated a greater abundance of species. This could be because of the particular life history traits associated with annuals, such as Senecio, which primes them for successful invasion and establishment, especially in dry sites like this study saw in VN. This invasive phenotypic plasticity of competing vegetation like Senecio could restrict the growth trajectories of Douglas-fir and put them at risk of mortality, especially at sites where water is more limiting.

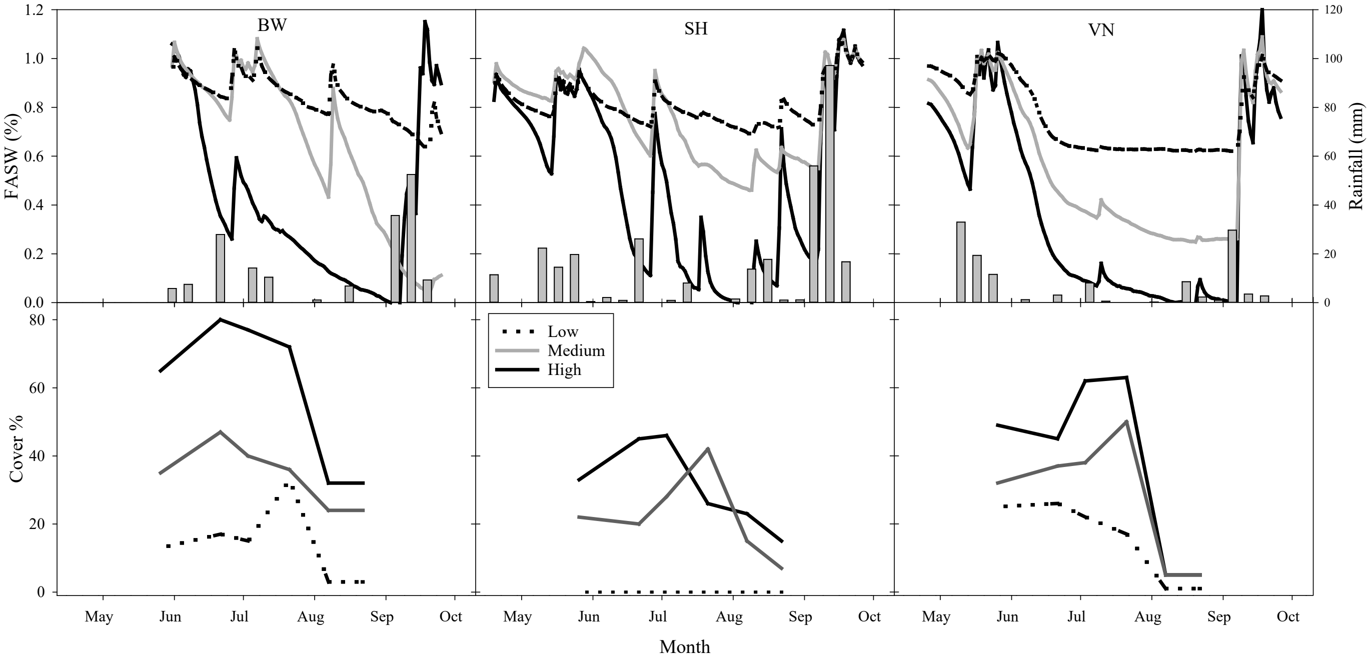

Figure 6. Seasonal dynamics of soil moisture (expressed as fractional available soil water of 0-30cm soil depth, FASW; upper panel) and Senecio abundance (expressed as cover percent; lower panel) on selected measurement points with low (dashed lines), medium (gray lines) and high (black lines) relative levels of Senecio cover% at the BW (left), SH (center) and VN (right) sites. On top panels, bars depict daily rainfall (mm).

The VN site had the quickest and earliest depletion of soil water resources. This drought effect could have even been more pronounced had there not been rain during early May, when the site was already experiencing steep reductions in VWC; the rain recharged the soil before it was depleted again, where it remained relatively stable at a FASW of about 10% to 60% for the rest of the drought season until the return of the rains in early September.

Newton and Preest (1988) note that it is particularly the Mediterranean climate of the PNW which leads to such a severe impact of competing vegetation. The drought season primes sites in this area to be intensely sensitive to the presence of competing vegetation. Therefore, the relatively severe drought conditions at VN can be considered in this context as intensifying the likely effects of Senecio competition for water and its likely impacts on Douglas-fir water stress through soil water depletion, as the results here show. The transpiration potential of Senecio, especially at VN, cannot be overstated in dry sites; Newton and Preest (1988) support this by noting that during the 3 to 5 months of summer drought, the transpiration of competing vegetation typically exceeds the water holding capacity of the soil; they note that if not controlled, this transpiration can exhaust the site of available water early in the growing season, which we saw in VN with the early steep depletion levels followed by an extended period of plateaued FASW. Ultimately Newton and Preest (1988) noted that this depletion of water reduced growth and induced mortality in the Douglas-fir.

Senecio Cover and Soil Moisture

Increases in Senecio abundance were associated with decreased soil moisture (Figure 6). There are many studies that have illustrated a similar intense depletion of soil moisture (e.g. Zedaker, 1981; Cole and Netwon, 1987; Newton and Preest, 1988) as a result of vegetation competition. The SH site is one example of the impact Senecio has on site water dynamics with increasing % cover: the 0% cover control probe is relatively flat over the entire growing season, having FASW above 0.8, while 20-40% cover of Senecio rapidly depletes FASW to 0 by the middle of August (Figure 6). This is likely because SH had the lowest ASW (14%). It is also interesting to note that the difference between 20-40% cover’s depletion of water was greater than the 0-20%, especially on the timing of depletion; this was seen at BW to the same severe degree, and to a limited degree in VN. This threshold effect is similar to that noted by Dinger et al. (2012), where levels above 20% competing vegetation had greater impacts on Douglas-fir than lower levels. This depletion on its own is associated with growth losses and the phenology of Douglas-fir above and belowground growth (Newton and Preest, 1988). These authors also noted that above-ground herbaceous plants were associated with 37% of the variation of water depletion, with the rest being depleted by Douglas-fir, drainage, and surface evaporation. This associated depletion is consistently more damaging in Mediterranean climates where light is abundant but moisture is limiting (Rosenzweig, 1968; Miller, 1981).

Independent of site, at some point during the growing season FASW was reduced to 0 in areas with high abundance of Senecio (Figure 6). The probe with the most depletion (highest % Senecio cover) at VN was below 20% FASW from Jun 14th to the end of the growing season. This extended the drought period by about a month compared to the other sites, both of which were lowered to about 20% by the middle of July (SH: 7/7; BW: 7/10). The frequency of rainfall events recharged the soil multiple times over the drought period; for SH, this occurred 4 times, and is the main reason the site soil moisture did not stay as near to 0 FASW for as long as the VN site did. It is also worth noting that even though BW had the highest average site Cover by Height (CxH) values (Figures 5 and 6), the FASW did not show the same effect as that seen at VN. This is likely because of the daily soil moisture recharge from fog at BW, which added moisture to upper layers of the soil and also moistened the Senecio leaves, thereby reducing the VPD and lowering evaporative demand for part of the day (Figure 4). This lower VPD then resulted in less water depletion for a given unit of Senecio cover compared to the other sites, which translates to a smaller reduction in FASW. The impact of fog on water stress has been studied for over 80 years, as Miller (1938) illustrated that significant amounts of solutes and water will enter leaves when the cuticle is only even moderately wet, as this increases permeability. It is therefore likely that at BW the impact of high levels of Senecio abundance were reduced by this fog.

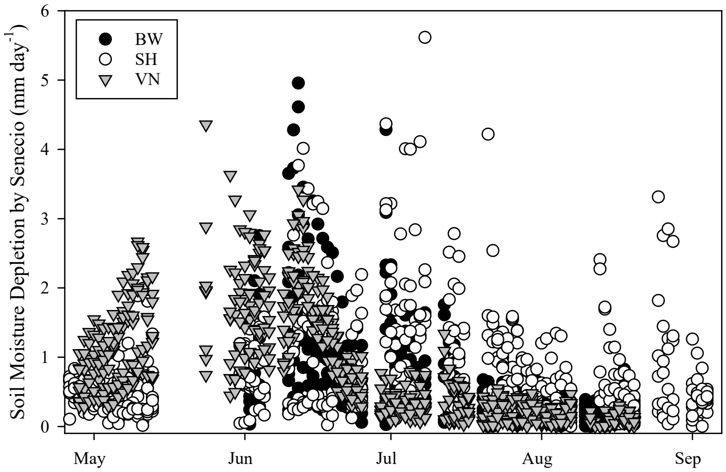

Figure 7. Seasonal dynamics in soil moisture depletion by Senecio in millimeters per day. Values are from each of the probes at the BW (filled circle), SH (open circle) and VN (grey triangle) sites. These probes had no trees within 1 m illustrating the theoretical depletion of Senecio. Retracted values represent days not accounted for due to rainfall at least two days before.

The wide variability shown in Figure 7 is related to the range of Senecio abundance observed. The VN site showed the earliest and most intense soil water depletion with a maximum loss of 4.5 mm day^{-1} during late May, which was soon after a rainfall event. However, even before this recharge, the amount of depletion was steadily increasing every day during early to mid-May. This peak at VN soon leveled off, which is likely associated with the competition-induced mortality shown in Figure 5 around 6/14. By this time, the site water levels had largely already been reduced below 20% FASW. There was therefore little water left to deplete, as the diminishing depletion levels illustrate.

As is consistent, VN had the earliest peak in depletion in late May, BW had the next peak (5 mm day^{-1} maximum soil moisture depletion) in early June, and SH had the latest peak in July with a maximum depletion of 5.6 mm day^{-1}. These values are not surprising, as Dinger et al. (2012) showed that Senecio had the highest transpiration rates (5.7 mmol H_20 m^{-2} s^{-1}) of four invasive annuals in their study during late June and early July in both irrigated and non-irrigated plots, showing how intensively Senecio can deplete sites of available water resources. Dinger et al.

(2012) also showed the same pattern of peak water use followed by senescence after the plants produced seed in early August. The maximum soil water depletion later in the season from the BW and SH sites are likely from the precipitation events which recharged the soil and enabled larger depletions than the VN site, where reduced rainfall made soil water much more limiting. This illustrates the combination of available water and seasonal dynamics: as water is more limiting, earlier peaks in growth and depletion occur while more available water extends the growing season. High levels of soil water reduction late in the season at the SH site can be attributed to the extended lifespan of Senecio at this site (Figures 5 and 6). There were such tolerable conditions for Senecio growth that a second cohort germinated and began to grow at SH. This could likely explain the continued depletion of soil water into early September, at least a month after the other two sites had reached their lowest levels.

Figure 8 illustrates the different amounts of cumulative water depletion of the top 30 cm soil at each site as a result of Senecio's presence from 5/31 to 9/4. There are no data for VN and BW past 8/22 because the majority of the Senecio had senesced at this point, while SH still had a large live population, and supported a second cohort into September. This figure shows that VN had the most intense and earliest depletion levels, with BW and SH having similar initial levels of soil water depletion, and SH continuing to deplete the site of soil water after BW and VN had leveled off. Although precipitation events excluded several days from our analysis which underestimates the average cumulative total, this nonetheless illustrates the intense pressure that Senecio puts on a dry site where moisture is limiting compared to wetter ones.

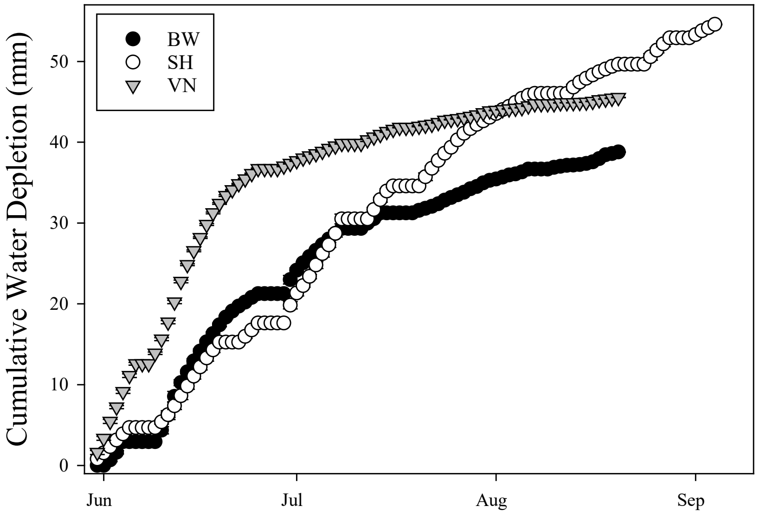

Figure 8. Average probe cumulative water depletion over the growing season at all three sites with standard errors. BW is the black circle, SH is the white circle, and VN is the dark grey triangle. Values were taken from the previous figure and summed for a cumulative illustration of total site water use.

At the VN site, across all eight soil moisture measurement points, the average total soil water depletion (water use by Senecio) was 46 mm for the 82 days of data recorded with living Senecio, having an average soil water depletion of 0.56 mm day^{-1}. 13.7 mm of rain occurred during this period. During the peak growing period (6/3 – 6/22; Figure 5), the average soil water depletion was 1.63 mm day^{-1}. During this period, average Senecio cover was 37%. For the rest of the growing season, soil water depletion by Senecio averaged 0.21 mm day^{-1}.

At the SH site, the average total soil water depletion was 55 mm (5/31 – 9/4; Figure 8), averaging 0.83 mm day^{-1}. During this period the site received 72.4 mm of rain and 29 days were excluded to avoid the effect of rainfall on soil water depletion. During the period between 6/3 and 6/22 (peak of Senecio growth, see Figure 5), the average soil water depletion was 1.0 mm day^{-1}. Average Senecio cover was 13% during this period.

At the BW site, average soil water depletion was 0.39 mm day^{-1} (5/31 – 8/22; Figure 8). During this period the site received 73.6 mm of rain. During the peak growing period of Senecio

(6/3 – 6/22; Figure 5), the average soil water depletion was 1.3 mm day^{-1}. During this period average Senecio cover was 36%. Over the rest of the growing season, soil water depletion by Senecio averaged 0.4 mm day^{-1}.

In general, less available soil moisture was observed in places with higher abundance of Senecio, but this relationship was different across sites. Figure 9 illustrates the take-home message of this project: as Senecio cover % increases, available soil water decreases. This figure focused on the month of July during peak Senecio abundance. It is worth noting that there was a difference in the FASW response at SH than the other two sites (Figure 9).

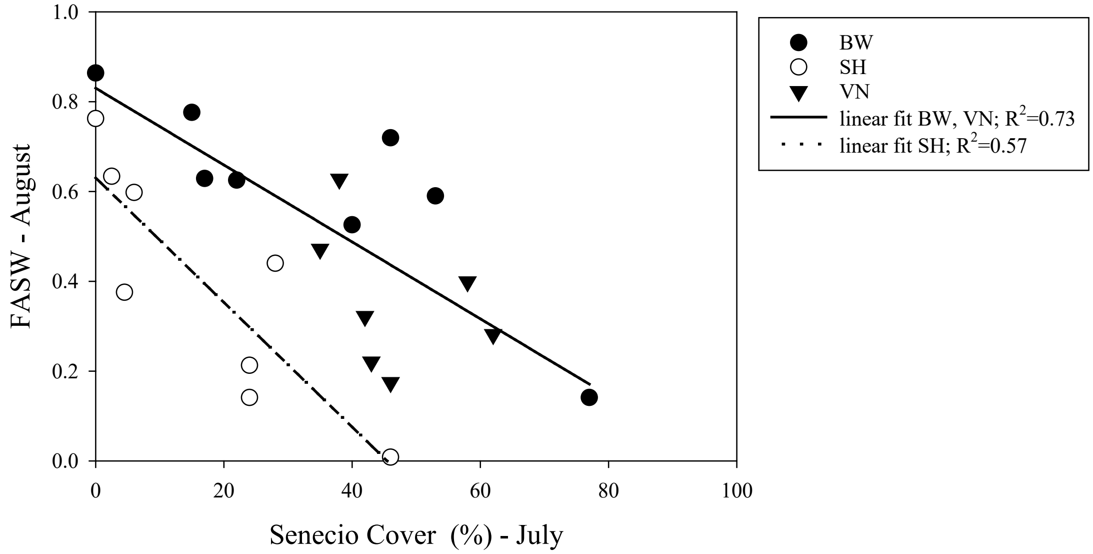

Figure 9. Relationship between cover percent measured in July and soil moisture (expressed as fractional available soil water, FASW) in August, for *S. sylvaticus* growing at the BW (filled circle), SH (open circle) and VN (filled triangle) sites.

The results shown in Figure 9 illustrate the need to control Senecio and regulate the amount of cover tolerated at sites in order to retain site resources for the crop trees. This figure shows that there are significant impacts of Senecio on FASW even at around 20% cover. As a result, letting even approximately 20% Senecio reside at a site results in a potentially 30% loss of FASW compared to total elimination of Senecio at 0% cover.

Conclusions

In this study we examined the effects of Senecio on soil moisture dynamics across sites with varying climate, soil, and Senecio abundance. Soil moisture probes surrounded by higher levels of Senecio had much higher rates of soil water depletion than those with less cover demonstrating the competitiveness and rapid resource utilization of Senecio. For Veneta, the dry site, this occurred earliest and to the greatest degree in July; for Burnt Woods, this occurred during August; for Sweet Home, our wettest site, the greatest correlation between Senecio cover and depletion was in early September. However, the degree of this impact differed across sites and over time, largely as a result of the atmospheric and soil conditions at the sites; i.e. the impacts were more extreme in the dry site than the wet sites, which is the result of the sand/silt/clay percentages and these impacts on water holding capacity. This pattern was also consistent with the cumulative and daily amount of soil water depletion in mm per day: the earliest and severest depletion occurred in VN, then BW, then SH. Furthermore, fractional available soil water was reduced to 35% from 65% in August with a Senecio cover of only 20% at SH. This effect was consistent with the other two sites, but not to the same extreme degree. The results from this study can help to inform management decisions on a site-specific context when deciding on the appropriate amount of control for different types and abundances of competing vegetation. Senecio presence is more deleterious and impactful at dry sites where water is a limiting resource than at wetter sites. This depletion of soil water and inducement of Douglas-fir drought stress can be mitigated operationally by prioritizing a spring release treatment at sites which have been, or are at risk of, being invaded by large amounts of Senecio.

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Chapter 3: Impacts of *Senecio sylvaticus* Abundance on *Pseudotsuga menziesii* Seedling Water Stress at Three Sites in Western Oregon

Introduction

To successfully buffer desirable species such as Douglas-fir seedlings against growth losses and mortality likelihood associated with competition, actions must be taken to ensure the availability of site resources for crop tree use. Competing vegetation, especially in sites where water is limiting, can have extreme physiological and economic consequences on crop trees if not adequately controlled (Dinger and Rose, 2009). This need to grow crop trees more quickly and efficiently is the result of different socioeconomic pressures for wood products, including fiber, fuel, structural material, and pulp (Parde, 1980; Jansen, 2014).

Understanding how trees grow optimally across different environments is useful in many different applications from industry to research, as an accounting of water use dynamics and growth rates is useful for estimating potential productivity and the carbon sequestration potential of a site. This includes an accounting of the tolerance of crop trees to vegetation competition, the degree of which differs across environments and species. Site water balance changes affect Carbon fixation rates through many routes, such as prohibiting water uptake or closing stomata during the day. Ultimately, a reduction in available soil water at a site has negative consequences for crop tree growth rates and homeostatic well-being; to what degree this negative consequence occurs is the product of atmospheric conditions, the amount of precipitation over the growing season, and soil textural qualities (Kramer and Boyer, 1995). It is important to continue developing an understanding of the link between competing vegetation's water depletion and crop tree drought stress, and how this link changes based on site conditions. This optimization of reforestation practices through vegetation management is a highly relevant contemporary topic, and the passage of a bill in this regard is currently in its adolescent legislative stages (e.g. last year's Oregon HB2020 and the current Cap-and-Trade Bill).

Chapter 2 illustrated the impacts of Senecio abundance on soil-water dynamics over the growing season across three sites. There were different levels of water depletion based on varied Senecio presence and site conditions. In this chapter, the relationship between soil water conditions, especially reductions over the drought period, and the water stress of Douglas-fir seedlings is discussed. This chapter shows the consequences of Senecio abundance on soil water dynamics and the relationship with water stress in different environments, both for the Douglas-fir and for Senecio. Analyses were done on predawn and midday water potential, soil moisture, and weather variables between and within sites to get an understanding of the variation of these relationships across geographic regions, from the cascade foothills to the coastal range in central Oregon. Senecio is abundant across these landscapes, and this chapter illustrates the impact this presence had on crop tree drought stress and the shortening of the growing season as a result; this occurred to varying degrees based on the amount of Senecio abundance, the atmospheric conditions and the weather patterns at each site.

Literature Review

Impacts of Competition on Water Dynamics

Data from the Vegetation Management Research Cooperative (VMRC) at OSU, as well as from other studies, has shown that weeds such as *Senecio sylvaticus* [L.] (Woodland groundsel, Senecio) are an intense competitor for and rapidly deplete soil water resources throughout the growing season (Dinger et al., 2012; Dinger and Rose, 2009). Competition for soil water resources between newly planted tree seedlings and aggressive early-seral plants, such as Senecio, can create drought conditions that impact tree seedling physiology, growth and likelihood of mortality. The Mediterranean climate of the Pacific Northwest (PNW) produces prolonged summer drought periods on many sites throughout the region that limits the growing season for crop trees and defines the vegetation community that can survive in this region (Powers and Reynolds, 1999). This drought condition can be exacerbated in newly established forest stands by Senecio-tree seedling competition for soil water, as Senecio has been observed to rapidly colonize regenerating forest plantations (West and Chilcote, 1968; Dyerness, 1973).

Water availability is one of the most important requirements for tree-seedling growth and development, as water is the main constituent of plant living cells, operates as a good solvent, and allows the movement of nutrients and carbohydrates throughout the plant, for example (Kramer and Boyer, 1995). Furthermore, a reduction in water availability and subsequent water stress reduces plant stomatal conductance and, hence, carbon fixation and growth (Khan, 1996). A long enough deficit in water status may have irreversible effects on photosynthetic machinery, induce permanent enzyme failure, and damage root and shoot systems as a result of extreme water potentials (Kramer and Boyer, 1995; Khan, 1996). It requires more energy to move water that has increasingly negative water potential values; the lower the water potential that is transmitted along this gradient into the xylem, the greater the chance of cavitation or embolism for the seedling (Sperry et al., 1988). A Douglas-fir seedling can survive and recover from several embolisms, but if the frequency of embolism continues unimpeded then eventually the damage becomes too much to repair, and total hydraulic failure occurs as a result of the tissue destruction (Fuchs et al., 1996). Even if the seedling does not die, this damage diminishes or precludes recovery, water uptake and use. For example, Unterscheutz (1974) showed that seedlings which were exposed to previous soil moisture stress had lower transpiration rates at the same low water potential than those which were stressed for the first time. Controlling competing vegetation to avoid this occurrence is therefore an essential operational consideration for having productive and healthy forests, as it improves long term growth patterns (Petersen and Newton, 1985).

Xylem Water Potential

Water potential is a metric referencing the ability of water to do work compared to free pure water at a standard pressure and temperature whose water potential is zero (Monson and Baldocchi, 2014). Water potential measures are useful metrics because water is one of the most important growth-limiting resources at a site, and its presence and changes over time are relatively easily measured. For example, water constitutes 80-90% of the fresh weight of herbaceous plants and about 50% of the fresh weight of woody-stemmed plants (Kramer and Boyer, 1995). Furthermore, for growth to occur through cell expansion, there must be adequate cell turgor which is necessitated by plant water status; water is also essential for driving gas exchange and fueling photosynthesis.

Water potential measures have been used as an index of water stress for many years with good results (Waring and Cleary, 1967; Running, 1976; Sands and Nambiar, 1984; Gonzalez-Benecke et al., 2018). Predawn water potential (Ψ_{PD}, MPa) is useful as a means of getting access to the relationship between plant and soil water status, as when the plants close their stomata, they achieve equilibrium with the soil during the night. The plant's Ψ_{PD} therefore shows the water status of the soil in the immediate vicinity that the plant is experiencing. Furthermore, midday water potential (Ψ_{MD}, MPa) is a useful index for assessing the stress experienced by a tree seedling during solar noon; the difference between these two values illustrates the impact of driving forces on transpiration, as a large difference indicates that much transpiration has occurred, or that the xylem is under intense pressure to do so. The degree of water potential, for Ψ_{PD} or Ψ_{MD}, illustrates the likelihood of cavitation, the extent of drought stress, and the subsequent photosynthetic efficiency the tree seedling is experiencing (Monson and Baldocchi, 2014).

The movement of water, including through plant absorption, occurs because of differences between water potentials along a gradient: the water moves from higher (less negative) to lower (more negative) water potentials spontaneously and passively. Beyond plant tissue status, the other two aspects of the gradient are the atmospheric and soil conditions. These conditions define how rapidly a plant transpires. This movement of water along the soil-plant-atmosphere gradient is only possible because of the continuous nature of the cohesive hydraulic system; if an embolism occurs, then the continuity of the gradient is disrupted and water will no longer move up the xylem.

The evaporation of water from leaves as a result of the stomata being open for gas exchange lowers their water potential, which causes the water in the xylem, at a higher water potential, to move into the leaves. This creates tension in the xylem, which is transmitted down into the roots; this transmission of tension allows passive absorption of water along the gradient. If the tension becomes too great and an embolism occurs, or the stomata close to protect against this, then the leaves will undergo dehydration and experience degradation of cell membranes, which becomes permanent as this dehydration becomes more severe (Kramer and Boyer, 1995). The extent of cell membrane disintegration dictates the potential recovery of the photosynthetic capacity of the plant when rehydration occurs. Kramer and Boyer (1995) note that photosynthesis may be inhibited for several days or longer after dehydration recovery because of embolism disruption of the water transport column and the inability of the guard cells to accumulate potassium, which causes incomplete stomatal opening. Furthermore, Newton and Preest (1988) found that weather, soil water, and time explained 80% of the variation in Douglas-fir xylem potential. All of these factors illustrate the feedback cycles that influence the significance of the amount and availability of water at a site, and the likely impact of this water availability on plant growth and health.

This research project investigated the degree of competitiveness of Senecio by analyzing soil moisture depletion and induced drought stress in Douglas-fir seedlings. Our results show that a greater abundance of Senecio translated to faster soil moisture depletion and more negative xylem water potential for both Ψ_{PD} and Ψ_{MD} of Douglas-fir seedlings. However, the degree of this impact differed across sites and over time, largely because of the atmospheric and soil conditions at the sites. The impacts of Senecio presence and water depletion were most severe in the dry (higher water deficit) site than the wet sites, which extended the drought season and induced intense water stress in Douglas-fir seedlings.

Objectives and Hypothesis

The goal of the research presented in this chapter was to quantify the effects of early seral competition by Senecio on Douglas-fir tree seedling water stress using predawn and midday water potential assessments across a range of sites in Western Oregon. This information can be used to support management decisions to effectively and efficiently control weed species, such as Senecio, that compete with crop trees.

This study hypothesizes that intense water depletion by Senecio will increase water stress in Douglas-fir seedlings to varying degrees across different environments. We predict that those seedlings with higher abundance of Senecio around them will show increased local soil water depletion, and have, as a result, more negative Ψ_{PD} and Ψ_{MD}. This effect will be most pronounced at the dry site (VN) compared to the two wetter sites (SH and BW).

Methods

Site Selection

Study sites were located in newly planted Douglas-fir plantations in areas expected to have high amounts of Senecio. After consulting with VMRC cooperators, three study sites were selected in order to capture a gradient of site conditions across western Oregon. All of the selected sites received a pre-planting fall site preparation (FSP) herbicide application; within each site, a uniform 0.3 ha (61 x 61 m) study area was identified and excluded from any further herbicide application. By excluding these areas from any post-planting spring release treatments, a large amount of Senecio was expected at each site.

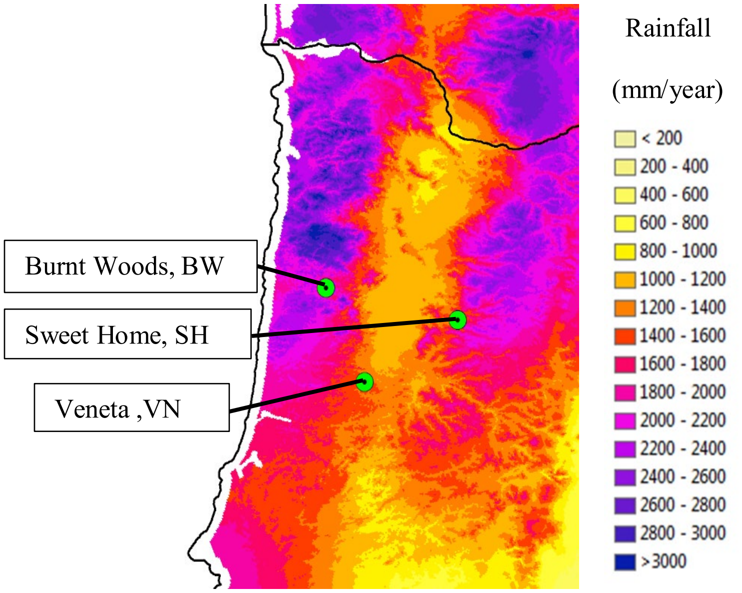

Figure 1. Location of study sites in western Oregon.

The first site is managed by Cascade Timber Consulting Inc. and is situated on a plateau near a steep slope overlooking the town of Sweet Home (SH, Figure 1, Figure 2a). This study site is located at 44°22'00.9"N 122°42'29.7"W in the central Cascade Range of Oregon at approximately 320 m above sea level and 109 km East of the Pacific Ocean. The site has a mean annual temperature of 10.8°C, mean annual precipitation of 1705 mm, and soils in the Peavine and

Kilchis-Harrington series defined as silty clay loam with stony loam (Wang et al., 2012; Soil Survey Staff, 2019). Observations also indicate that the soil has some areas that contained significant gravel and coarse material, including decomposing cedar. This site had the highest average soil clay content (36%), the lowest sand content (30%), the highest field capacity (0.39 cm^3 cm^{-3}), and lowest available soil water (ASW; 0.14 cm^3 cm^{-3}) of the three sites. This was our intermediate site, as it was neither extreme in temperature nor relative humidity. The site was planted with bareroot plug+1 Douglas-fir seedlings. The tank mix used in FSP included 2 qts. of glyphosate, 16 oz. of imazapyr, 4 oz. of Oust Extra and 8 oz. of MSO.

The second site is managed by the Oregon Department of Forestry and is located on a steep SE facing slope near Burnt Woods, OR (BW, Figure 1, Figure 2b). This study site is located at 44°35'14.2"N 123°40'57.0"W in the Coastal Range and is approximately 410 m above sea level and 35 km from Pacific Ocean. The site received a broadcast prescribed burn before planting, has a mean annual temperature of 10.2°C, mean annual precipitation of 2075 mm, and soils in the Preacher-Bohannon-Slickrock complex (Wang et al., 2012; Soil Survey Staff, 2019). This soil texture consists of loam weathered from sedimentary rock types, loam from sandstone, and Slickrock gravelly loam. This was our wettest site over the sampling period. This site also had the highest average soil sand percentage (36%), lowest clay content (30%), and highest ASW (0.16 cm^3 cm^{-3}) of the three sites. The site was planted with styro 20 containerized Douglas-fir seedlings. The tank mix used in FSP included 2 qts. of glyphosate and 4 oz. of Oust Extra.

The third site is owned by Roseburg Forest Products Inc. and is located near Veneta, OR (VN, Figure 1, Figure 2c). This study site is located at 43°56'25.3"N 123°23'58.3"W in the south-central valley and is approximately 266 m above sea level and is 65 km from the Pacific Ocean. It has a mean annual temperature of 11°C, mean annual precipitation of 1422 mm, and soils in the

Peavine series defined as a silty clay loam (Wang et al., 2012; Soil Survey Staff, 2019). This site had the highest average soil silt content (38%), and the lowest wilting point ($0.22\ cm^3\ cm^{-3}$). This was our dry site and it also had the most extreme weather conditions: highest temperatures, lowest relative humidity (highest VPD), and the least amount of rain. The site was planted with bareroot plug+1 Douglas-fir seedlings. The tank mix used in FSP included 2.25 qts. of glyphosate 5.4, 4 oz. of Oust XP and 1 oz. of MSM 60.

Senecio and Douglas-fir Xylem Water Potential

At each site, a circular study area of 0.3 ha was identified with uniform terrain conditions and varying abundance of Senecio. The study area was divided into two rings: the inner ring had a radius of 21.5 m and the outer ring had a radius of 30.5 m. Each of these rings were divided into four quadrants, resulting in eight octants of equal area (Figure 2). One soil moisture TDR probe was installed in each octant at a random azimuth and distance from the central point (see Chapter two; this probe data in not shown in this chapter). Within each 0.3 ha circular plot, 16 Douglas-fir seedlings growing in varying amounts of Senecio were selected and labeled for drought stress measurements (Figure 2). Two seedlings per octant were randomly selected that were near Senecio percent covers in the categories of 0-25%; 26-50%; and >51%. These ranges were chosen to get a balanced distribution of seedling samples from each cover percent category.

The 16 Douglas-fir seedlings at each site were used for monthly measurements of Ψ_{PD} and Ψ_{MD} between June and September using a pressure chamber (Model 600, PMS Instrument Co., Albany, OR). For Ψ_{PD} measurements, one live branchlet from each seedling was excised with a razor and put into a foil-laminated zip-lock bag (PMS Instruments Co., Albany, OR). Measurements were taken within 2 minutes after branchlet excision. Following the same protocol, Ψ_{MD} measures were taken as well during solar noon at each measurement day. Additionally, five

Senecio samples were measured for Ψ_{PD} and Ψ_{MD} in order to compare water stress of both the crop tree and the invasive herbaceous species.

Additionally, at each site, for both, Douglas fir and Senecio, we computed water stress integral (WSI, MPa day) following work by Myers (1988). WSI is the summation of xylem water potential (Ψ_{PD} or Ψ_{MD}) for each day over the sampling period. We used 4 measurements (June-September) for each site, each with corresponding time-steps as the number of days between measurements, to calculate WSI using the following formula:

$$WSI = \sum (\Psi_{i,i+1} - c) \cdot n$$

where $\Psi_{i,i+1}$ is the mean Ψ for the interval i,i+1; c is the datum value or maximum (least negative) Ψ measured; and n is the number of days per interval. We computed WSI using both, Ψ_{PD} (WSI_{PD}) and Ψ_{MD} (WSI_{MD}).

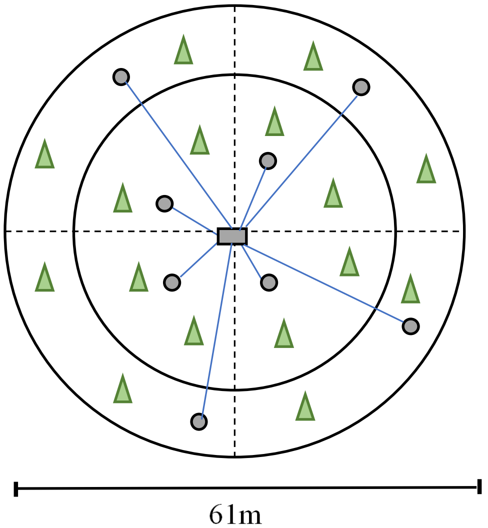

Figure 2. Diagram of sensors deployment in the study area (0.3 ha). Soil moisture sensors were deployed in two rings with the same area. The central grey rectangle represents the weather station with a datalogger. Gray circles represent the 8 soil moisture sensors (data not used in this chapter). Green triangles represent the 16 Douglas-fir seedlings where soil moisture and water potential were assessed.

Soil Moisture and Weather

At the central point of the circular plot (Figure 2), a weather station and datalogger (CR300, Campbell Scientific, Logan UT) were installed to measure and collect all soil moisture and weather information (all data was recorded at 30 minute intervals). Weather measurements included global radiation, air temperature, relative humidity and rainfall. Given an operational spacing of 3 x 3 m, there were about 310 Douglas-fir seedlings per study area at each site.

In order to correlate soil moisture and seedling water potential, measurements of soil volumetric water content were also taken adjacent to the 16 seedlings (15 cm from stem; two measurements per seedling) on each measurement date using a handheld TDR soil moisture sensor (HS2, Campbell Scientific, Logan UT). Readings from the handheld TDR probe were calibrated with *in situ* gravimetric measurements of volumetric water content using 8 soil cores taken from each site (AMS, bulk density soil sampling kit).

Statistical Analysis

Analyses were done using SAS version 9.4 (2020) for model building and statistical tests (PROC GLM and PROC NLIN). A linear regression was used to correlate Senecio cover by height and Douglas-fir Ψ_{PD}. Another linear regression was used to calibrate handheld TDR VWC readings (Appendix, Figure A3.1). Model fitting was done using SAS for VWC and Ψ_{PD}. Two-Way Analyses of Variance (ANOVA) with Tukey Post-Hoc tests were used to determine the effect of species, site, and the interaction of species by site for Ψ_{PD}. Results are shown in Figure 4. All significance tests used $\alpha = 0.05$. Sigmaplot version 14 (Systat Software, Inc. San Jose, CA, USA) was used to make all figures.

Results and Discussion

Weather Conditions

Weather stations collected data at SH and VN beginning in mid-April. Our original third site was moved in May when little-to-no Senecio abundance was observed; therefore, measurements began in late May for BW. There were differences between sites for the weekly mean weather variables from April to late September (Figure 3). The VN site had the highest temperatures, lowest relative humidity and least amount of rainfall, with almost no rainfall from June 1st until the beginning of September. The SH and BW sites both had more rain overall and experienced heavy rain events in June which recharged the soil and helped to reduce the length and intensity of the seasonal drought. Over the shared site measurement period (5/31-9/27), the VN site had 62 mm of rain, while the SH and BW sites had 227 mm and 171 mm of rainfall, respectively. The mean growing season temperature for VN, SH and BW sites was 16.8, 16.1, and 16.2 ºC, respectively. The mean RH was 72, 75 and 81% for the VN, SH and BW sites, respectively. This data reflects that drought conditions were more intense at the VN site than the SH or BW sites.

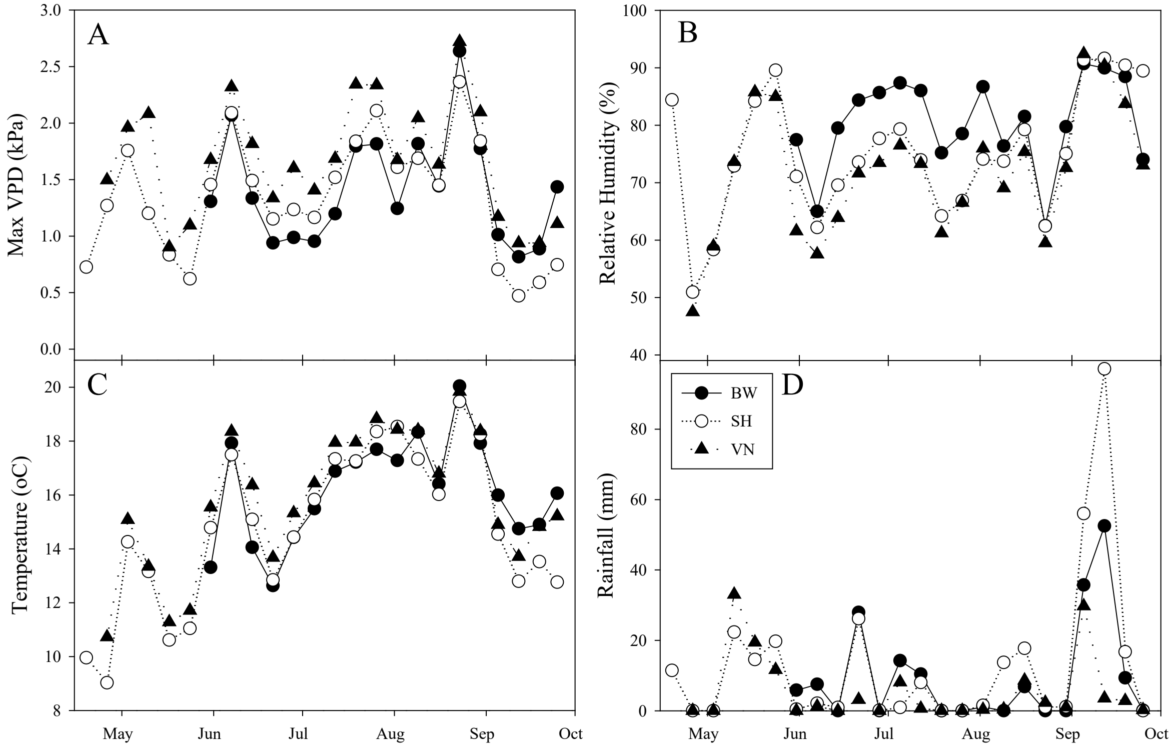

Figure 3. Weekly mean: A) maximum VPD, B) relative humidity, C) air temperature and D) total rainfall, for the BW (filled circle), SH (open circle) and VN (filled triangle) sites.

Senecio and Douglas-fir Xylem Water Potential

Seasonal variation in xylem water potential is shown in Figure 4. There was an interactive effect of time (month) and site on Ψ_{PD} (P=0.026) and Ψ_{MD} (P=0.071) across species, meaning that the plant water status was different between Douglas-fir and Senecio for the different sites at different dates during the growing season. For instance, at the BH and SW sites there were no significant differences in Ψ_{PD} between species at any time during the growing season, but at the VN site during late summer (August and September) there were significant differences, with Douglas-fir seedlings having more negative Ψ_{PD} than Senecio (P<0.001 and P=0.009, respectively). Differences in rainfall, evaporative demand and Senecio abundance may explain the differences observed. There were differences between species Ψ_{MD} at all the sites and this effect was strongest at the end of the summer. The BW and SH sites showed significant differences in Ψ_{MD} between species for August and September ($P<0.003$), but not for Ψ_{PD}. It is interesting to note that at the VN site, the species significantly differed for every single measurement date with data ($P<0.001$).

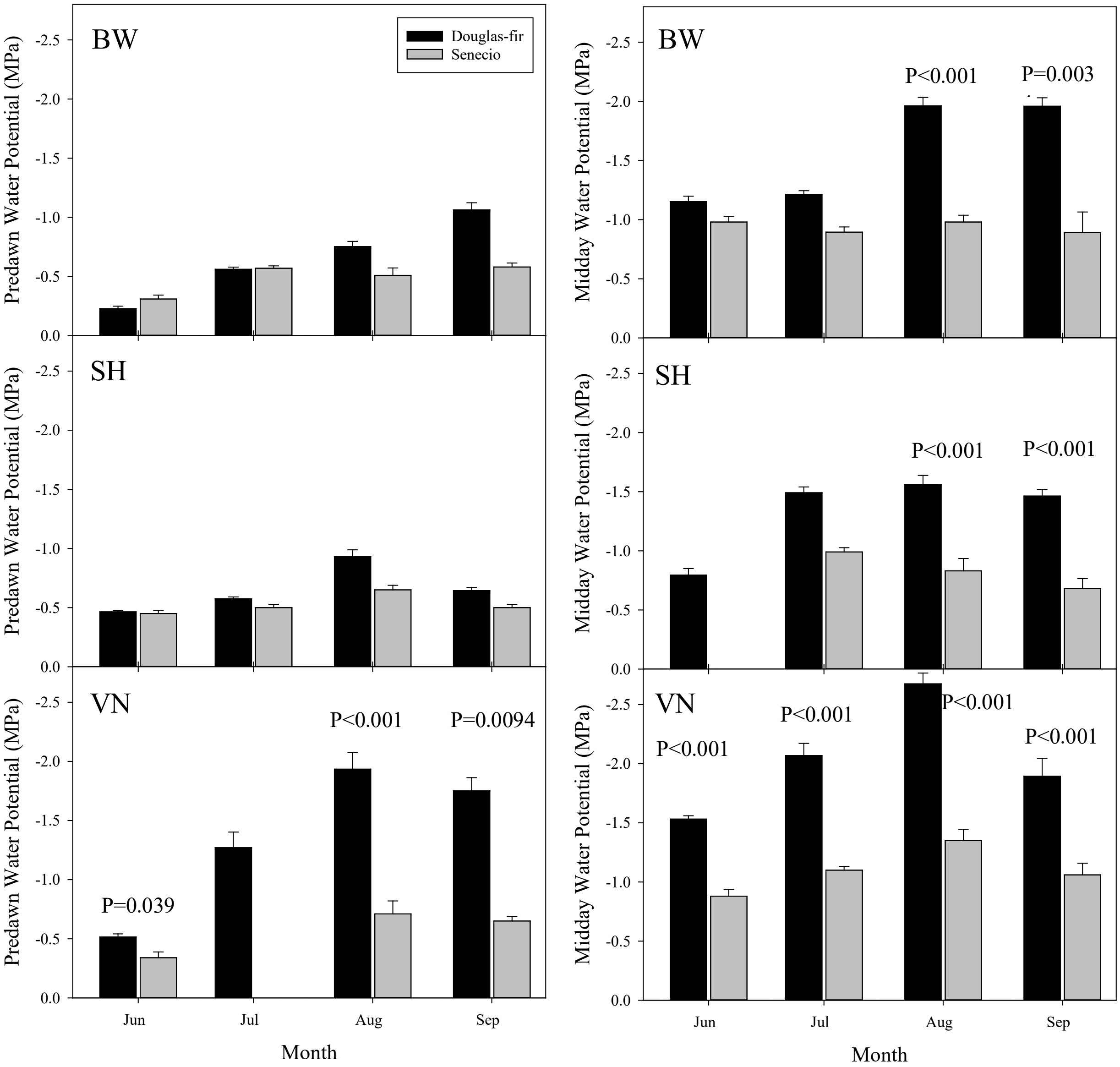

Figure 4. Predawn (left) and midday (right) xylem water potential of Douglas-fir (black bar) and Senecio (grey bar) growing at BW (upper panel), SH (middle panel) and VN (lower panel) sites. Error bars represent standard error. P-values for significant differences between species are shown on top of each pair of columns. Water potential was not measured for Senecio in June at the SH site and in July at the July site.

Senecio had a much narrower response of xylem water potential for both Ψ_{PD} and Ψ_{MD} over the growing season compared to the Douglas-fir seedlings, illustrating a reduced degree of water stress. Douglas-fir's elevated water stress has likely consequences at VN in August, where the average Ψ_{PD} and Ψ_{MD} values were -1.9 MPa and -2.6 MPa, respectively, illustrating loss of stomatal conductance; this is likely the combination of atmospheric demand as well as water depletion by Senecio. For instance, studies have shown that Douglas-fir can achieve maximum stomatal conductance and photosynthesis rate when Ψ_{PD} is above -1.0 MPa while decreasing beyond this level inhibits photosynthesis to 25% of maximum at -2.0 MPa (Brix, 1979). The long-term consequences of enduring states of water stress such as those seen at VN has been shown in previous studies (e.g. Havranek and Benecke, 1978; Newton and Preest, 1988). For instance, Newton and Preest (1988) showed that gains in tree volume at 5 years were correlated ($R^2=0.77$) with the difference in xylem water potential and the threshold of -2 MPa being breached, past which photosynthesis ceased and long-term growth consequences occurred. Because VN, on average, breached this threshold during July, August and September for Ψ_{MD}, and August and September for Ψ_{PD}, there are likely losses in volume accumulation. Although the degree of this loss of volume cannot be quantified at this time, future projects could evaluate the growth consequences of Douglas-fir as a result of Senecio induced drought stress.

The relationship between Douglas-fir Ψ_{PD} and soil volumetric water content is consistent with other results (Figure 5). For the SH site, when VWC is greater than 0.35 cm^3 cm^{-3}, Ψ_{PD} will have values larger than -0.5 MPa. When VWC reached values of about 0.15 cm^3 cm^{-3}, Ψ_{PD} will reach values below -1.5 MPa. At the VN site, when VWC is greater than 0.23 cm^3 cm^{-3}, Ψ_{PD} will have values larger than -0.5 MPa, while at the BW site, a similar Ψ_{PD} can be found when VWC is around 0.15 cm^3 cm^{-3}. The BW and VN sites showed similar behavior when the soil is dry: Ψ_{PD}

around -1.5 MPa is expected when VWC reaches 0.07 cm^3 cm^{-3}. Differences across sites likely reflect differences in soil texture and organic matter content. For instance, the SH site has, on average, the highest soil clay content (36%) and the lowest sand content (30%). There are therefore differences between the sites in the responsiveness of the Douglas-fir to changing water conditions, which is the product of the interaction of Senecio presence, water depletion, soil qualities, and atmospheric conditions.

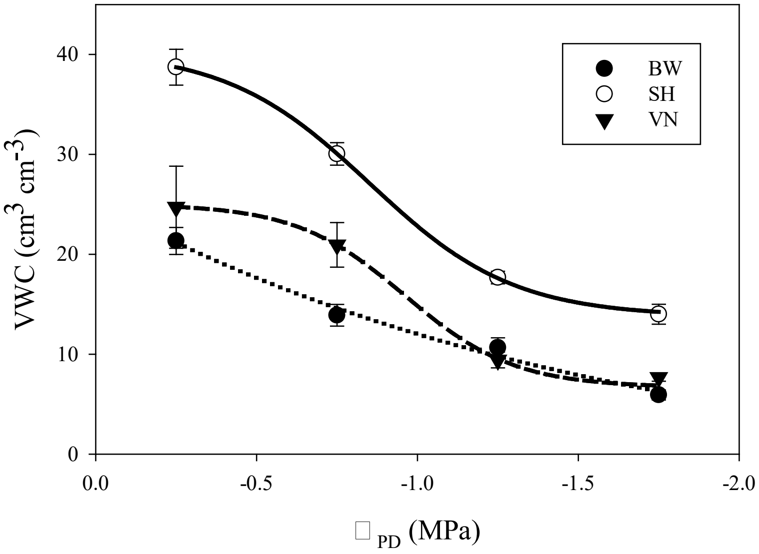

Figure 5. Relationship between Predawn Water Potential (Ψ_{PD}, MPa) and soil volumetric water content (VWC, cm^3 cm^{-3}) for Douglas-fir seedlings growing at BW (filled circle), SH (open circle) and VN (filled triangle) sites. Curves fitted: black line (SH), dashed line (VN), and dotted line (BW). Calibration procedure for ASW shown in Appendix Figure A3.1.

WSI_{PD} differences were significant for site, species, and the interaction between species and site ($P<0.0001$) (Figure 6). WSI_{MD} differences were significant for site ($P<0.0001$) and species ($P=0.0008$), but not for the species and site interaction ($P=0.19$). In early September Douglas-fir seedlings growing at the VN site had a WSI_{PD} 2.4 times larger than those seedlings growing at the BW and SH sites (1.4 vs. 0.57 and 0.58 MPa day, respectively). However, the WSI_{MD} was only 1.5 times greater in VN in September compared to BW and SH (140 vs 97 and 89 MPa day, respectively). This lack of increase in WSI_{MD} over WSI_{PD} values for VN shows that the Douglas-fir were already undergoing stomatal closure, and were unable to conduct gas exchange to the same degree compared to BW and SH, which saw a greater relative increase.

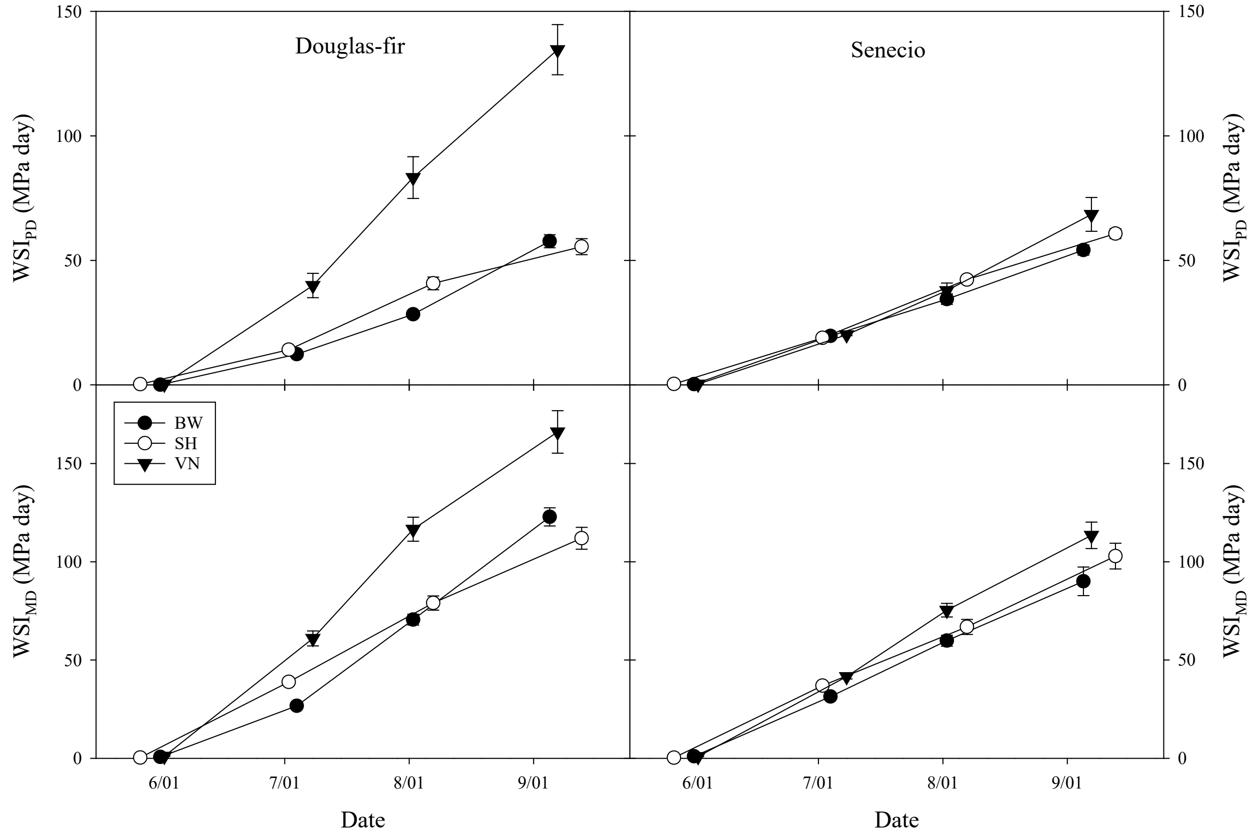

Figure 6. Seasonal dynamics of predawn (WSI_{PD}, upper panel) and midday (WSI_{MD}, lower panel) water stress integral for Douglas-fir (left) and Senecio (right) growing at BW (filled circle), SH (open circle) and VN (filled triangle) sites.

For Senecio, both the magnitude and the difference between WSI_{PD} and WSI_{MD} was less than for the Douglas-fir, especially compared to the VN Douglas-fir. Across sites, at the end of the growing season, WSI_{MD} for Senecio was approximately 1.7 times greater than WSI_{PD}. Compared to the Douglas-fir, which showed a steeper increase in WSI, Senecio was relatively drought-free over the growing season. As the significant interactive WSI_{PD} site by species effect shows

(P<0.0001), there were similarities for the sites between species for SH and BW for Douglas-fir, and all three sites for Senecio. The Douglas-fir and Senecio were both around 0.6 MPa at the end of the sampling period for SH and BW, while VN Douglas-fir illustrated a much larger effect of water stress at 1.4 MPa. Douglas-fir at VN, the dry site, drove the differences between the sites and species, as its values were more than twice as much as the other species and sites. It is therefore at the dry site that targeted elimination of Senecio must be undertaken, as the Douglas-fir showed a massive increase in WSI while the Senecio at the same site in the same conditions was hardly different compared to SH and BW.

The effect of Senecio abundance on Douglas-fir water stress is dependent upon the site characteristics, namely, available soil water and evaporative demand (Figure 7). For the VN site this effect was strongest: for every increase of 10 CxH of Senecio, Douglas-fir Ψ_{PD} decreased 0.5 MPa ($P<0.0001$; $R^2 = 0.57$). In sites such as VN with limited rainfall experienced during this study, having 30% cover of 1 m tall Senecio will result in the Douglas-fir seedlings having Ψ_{PD} of -1.7 MPa. For BW and SH, there was no relationship between Senecio abundance and Douglas-fir water stress for the month of July; however, similar patterns were seen in August for BW, and September for SH. However, VN had the greatest fit (highest R^2) as well as highest magnitude of elevated $\Psi_{PD.}$ Therefore, over the growing season, the effect of Senecio presence was different for each of the sites at different times (Figure 4).

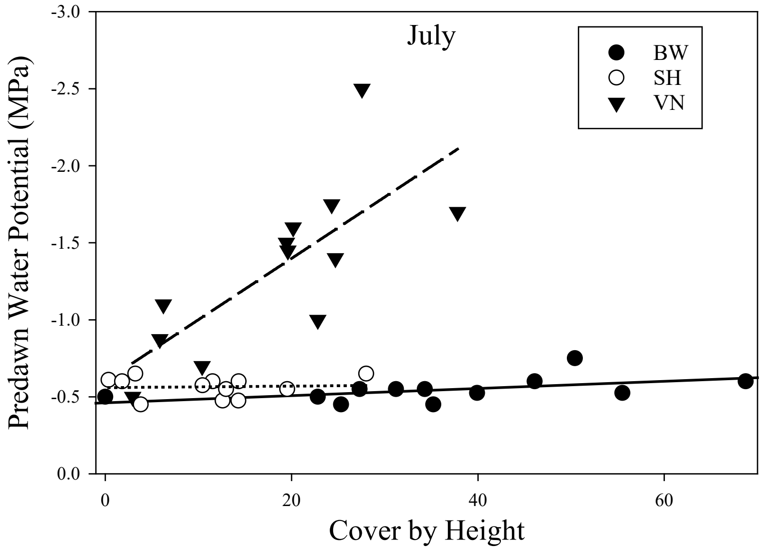

Figure 7. Relationship between Senecio Cover x Height (CxH) and Predawn Water Potential (Ψ$_{PD}$, MPa) for Douglas-fir seedlings growing at BW (filled circle), SH (open circle) and VN (filled triangle) sites).

The overall degree of magnitude difference for Ψ$_{PD}$ shows that there is variation between sites, regardless of Senecio abundance, as a result of atmospheric and soil conditions; however, the intense slope difference in July at VN shows that every unit increase of Senecio CxH is associated with a much more negative Ψ$_{PD}$ value. These results illustrate the continuing evidence that the timing of Senecio presence in combination with the amount of available soil water at a site dictates the impact on Douglas-fir drought stress. Newton and Preest (1988) discussed the importance of this timing, noting that xylem water potential stress relief, as a direct result of controlling competing vegetation and retaining site soil water, was associated with almost a four-fold gain in stand volume within the first 3 years. Furthermore, Havranek and Benecke (1978) showed that Douglas-fir can grow rapidly on dry sites with extreme heat and drought on clay loam soils, but only in the absence of competing herbaceous vegetation; the likely growth losses of VN could therefore have been ameliorated by the eradication of Senecio before July.

Conclusions

In this study we examined the effects of Senecio on drought stress inducement across sites with varying climate, soil, and Senecio abundance conditions. The degree of Senecio abundance impact on Douglas-fir drought stress was more pronounced at each site only during periods when ASW was depleted: July for VN, August for BW, and September for SH. In general, the results from Chapter 2 and 3 showed that as Senecio abundance increased, VWC decreased; as VWC decreased, Ψ_{PD} became more negative. The results from this study can help to inform management decisions on a site-specific context when deciding on the appropriate amount of control for different types and abundance of competing vegetation. Senecio presence is more deleterious and impactful at dry sites where water is a limiting resource than at wetter sites. This depletion of soil water and inducement of Douglas-fir drought stress can be mitigated operationally by prioritizing a spring release treatment at sites which have been, or are at risk of, being invaded by large amounts of Senecio.

Appendix:

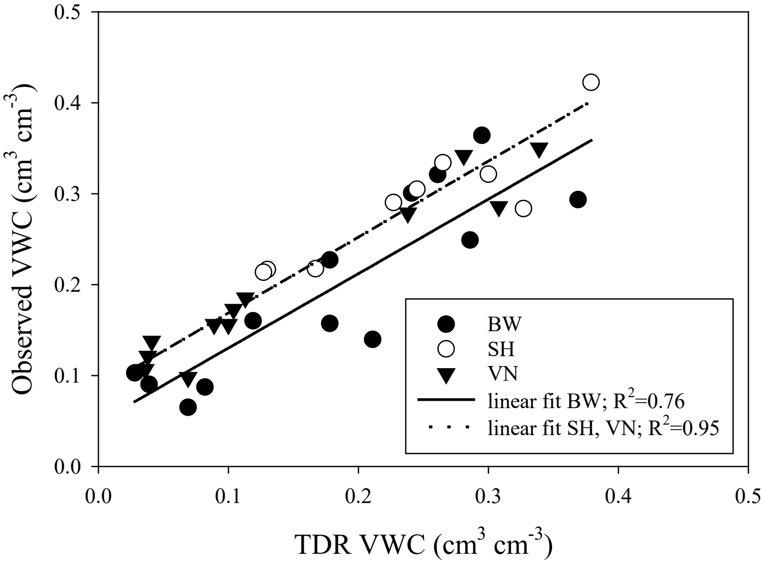

Figure A3.1. Calibration procedure for observed VWC and handheld TDR VWC illustrating the different site equations for the under and over-estimation of VWC.

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Chapter 4: Biomass and Root Architecture Variability of *Senecio sylvaticus* and *Pseudotsuga menziesii* across Three Sites in Western Oregon

Introduction

Water availability is of paramount importance for plant growth and survival. Several hundred grams of water are required to produce a single gram of dry plant matter and over 95% of this water is lost by transpiration. Worldwide more plants are injured or killed by dehydration through excessive transpiration than by any other single cause (Kramer and Boyer, 1995). Understanding how trees respond to environmental factors is useful in many different approaches from academic research to industrial applications, as an accounting of Carbon fixation and water use dynamics is useful for estimating the potential productivity and health of a site. Optimal growing conditions are compromised by many factors, including drought stress, which can be augmented by the abundance of competing vegetation. Therefore, ensuring that crop trees are free to grow by accounting for the likely impact of competing vegetation on site water balance is important from a legal standpoint (e.g. Oregon Forest Practices Act) as well as an operational one.

Because of changing climate trends in the Pacific Northwest (PNW) towards warmer and drier summers (Hamlet et al., 2007), the optimal forest establishment and growth question exists in an uncertain context; if these trends are correct, then management planning needs to account for the likely impact this increase in evaporative demand will have on crop tree growth patterns. These changing climatic patterns will likely increase the competitiveness of any given amount of competing vegetation through increased transpiration as a result of atmospheric drivers. The occurrence of drought is not inconsequential: drought is considered to be one of the major abiotic stressors limiting achievable plant growth (e.g. Rowland et al., 2015; Lambers, Chapin, and Pons, 2008). The Intergovernmental Panel on Climate Change (IPCC) stated that increasing air temperature and CO_2 concentrations will affect forest growth and productivity (Bernstein et al., 2007; Scheneider et al., 2007; IPCC, 2013). Beyond the average expected increases in temperature, there is also expected to be an increase in the frequency and intensity of heat waves which can severely limit growth and, potentially, can kill young trees (Meehl and Tebaldi, 2004; Boeck et al., 2010; IPCC, 2013). These increases in temperature could also augment Carbon sequestration by shifting Carbon to different metabolic pathways (Jansen et al. 2014). Although Douglas-fir is considered relatively resilient against increased environmental stressors (Gonzalez-Garcia et al., 2013), seedlings will likely be more strongly impacted than mature trees because of reduced root extension and concomitant small water absorbing area (Netwon and Preest, 1988; Gessler et al., 2013).

The allocation of resources to different plant structures and functions is the central premise of life history theory, and a better understanding of these allocation pathways can help determine the optimal growing conditions that promote plant establishment and health, especially as a high degree of variability exists between woody-stemmed, perennial, and annual herbs (Poorter et al., 1990; Weiner, 2004; Eziz et al., 2017). In support of this, Chan et al. (2003) found that competition among plants is a fundamental determinant of the size of different plant parts. The optimal partitioning theory states that the plant will allocate more resources to the part of the plant that is experiencing a growth-limiting restriction; if water is limiting for a plant, for instance, then more root allocation will therefore occur (Poorter et al., 2012). Biomass is considered to be the most accurate and feasible allocation product to measure the allometric pathways in plants (Harper and Ogden, 1970; Bazzaz et al., 1987).

Forest vegetation management (FVM), usually in the form of herbicide use, effectively buffers trees from vegetation competition for light, water and nutrients. Many of the herbicides used in pre-planting fall site preparation herbicide treatments (FSP) throughout the PNW do not effectively control Senecio. Due to this, it is common for sites that received a FSP treatment but no post-planting spring release herbicide treatment (SR) to be colonized by Senecio during the first growing season (Dinger et al., 2012). Some ways to mitigate the impacts of competition at the seedling level are to augment morphological and physiological plastic traits, such as lowering stomatal conductance, increasing water use efficiency, shifting allocation patterns, and having lower tissue turnover (Balandier, 2006; Goldberg, 1990; Kochy and Wilson, 2000; Peltzer and Kochy, 2001). Understanding to what degree different species and types of vegetation utilize these plastic pathways has important management implications.

Literature Review

Vegetation Biomass Estimation and Partitioning

Estimating vegetation biomass has many ecological applications, as it can help quantify the degree of species occupancy at a site, assess crop value, site productivity, fire and successional impacts, and regeneration (Catchpole and Wheeler, 1992). Visual estimates of plant cover have been well correlated with biomass estimation for ground cover vegetation species (Yarie, 1980; Röttgermann et al., 2000). Regression parameters for calculating biomass functions are estimated using a series of destructively sampled points to link biomass to the variables of interest.

When describing allocation strategies for avoiding mortality or tissue damage associated with drought, there are two general strategies: drought avoidance and drought tolerance; within the latter, there is desiccation avoidance (where low xylem water potential, Ψ, is prevented or postponed) and desiccation tolerance (where low Ψ is endured without loss of viability) (Kozlowski, 2002). Some specific examples of this are when foliage is shed, rapid closure of stomata during drought, development of leaf waxes, low resistance to water flow in vascular stem tissues, extensive root growth, and high root to shoot ratios (Kozlowski and Pallardy, 1997).

When plants grow on poor sites they can be generally expected to allocate more photosynthate products to root production than those that grow on higher quality sites where moisture is not as limiting (Kozlowski 2002; Ibrahim et al., 1997). For example, a study by Keyes and Grier (1981) showed that Douglas-fir seedlings growing at a poor site allocated 36% of total NPP to roots, while those growing on better sites only allocated 8% of NPP. Tillman (1985) showed that biomass allocation shifts are the direct result of plant response to competition; this plastic quality of plants is an important consideration in the context of a changing climate and how competition within a site is augmented by decreased water availability in the future. Water availability is augmented both by plant use and the influence of atmospheric conditions.

The balanced-growth hypothesis, or optimal partitioning theory, is one way to interpret plant responses to limiting resources (Shipley, 2002). Kramer and Boyer (1995) discuss the general trend of plants responding to dry soils by emphasizing root growth over shoot growth (e.g. Gales, 1979; Malik et at., 1979; Stewart and Nielsen, 1990). In support of this, Radosevitch and Osteryoung (1987) found that the establishment of a robust and efficient root system is essential for the success of Douglas-fir seedlings in xeric environments.

Eziz et al. (2017), in a large meta-analysis, found that across plant types drought caused an increased allocation to root mass by 9% and a decrease in stem, leaf, and reproductive mass fractions by 6%, 2%, and 8%, respectively. Furthermore, the same authors showed that biomass allocation across type was not consistent; for annual herbaceous plants, such as Senecio, the root mass fraction was increased much more (10% v/s 5%) in response to drought than woody-stemmed or perennial herbs. This tradeoff was paid for by a greater decrease in reproductive mass fraction in woody-stemmed and perennial plants; this is an efficient strategy because woody-stemmed and perennials have later years to compensate for a drought season where they prioritized growth over reproduction. However, successive drought years, which may occur with greater frequency in the future (IPCC, 2013), could therefore favor the annual life history strategy while lowering perennial and woody-stemmed plant fitness. Eziz et al. (2017) also found that woody-stemmed plants allocated less energy to leaf mass compared to herbaceous plants when resources were scarce, which has impacts on transpiration rates between plant types.

Growth and Allocation Plasticity

Much previous work on the relationship between competing vegetation and crop tree growth patterns have focused on wood volume production (e.g. Wagner et al., 2006), while fewer studies have focused on biomass partitioning changes in response to competition. Petersen et al. (2008) is one example of this latter research where they discussed the different allocation patterns of Douglas-fir growing with and without vegetation control; they found that those trees growing without competition had significantly larger stem, branch, foliage, and overall biomass than their counterparts of the same size stem diameter growing with vegetation competition. Furthermore, Tesch et al. (1992) found that Douglas-fir total biomass was reduced by 90% in moderate shrub competition and 95% in heavy competition compared to no competition seedlings; in addition to this, they found that stem volume was 10 times that of seedlings experiencing competition.

Although little research has focused specifically on *Senecio sylvaticus*'s water use and biomass partitioning, more work has been done on its closest relative: *Senecio vulgaris*. For instance, Bernston and Woodward (1992) showed that *S. vulgaris* responded to both increased CO_2 and soil moisture levels: at 350 ppm CO_2, average root length was 2.0 cm and 4.3 cm in the dry and wet sites, while at 750 ppm, root length was 4.6 and 11.7 cm in the dry and wet sites, respectively. The authors posited that this demonstration of root plasticity illustrates a high exploitive efficiency—high ratio of soil exploited per unit root length—and explains its advantage in water-limiting environments. The authors posit that the distance between primary and secondary roots, as well as diverse branching angles illustrated a highly efficient water exploiting system. When water is available, this high exploitive efficiency offers the plant greater transport efficiency given the network of roots already in place. In general, herbaceous vegetation is associated with greater depletions of soil water. This could be because of the greater proportional allocation of biomass to foliage and roots when compared to woody species. For instance, Kramer and Boyer (1995) discussed the different proportions of water used by a field filled with herbaceous plants that used 60 to 90% of the incoming precipitation compared to a forest in Appalachia that used only 25 to 35%. It is therefore not just Senecio's intense water use capabilities, but also its responsiveness to environmental cues that primes it to colonize and outcompete other vegetation, especially newly planted Douglas-fir seedlings. These results illustrate that species in the genus Senecio are likely to increase in competitiveness given the projected increase in atmospheric CO_2 concentration in the future (IPCC, 2013).

Objectives and Hypothesis

The objective of this chapter's research was to quantify biomass partitioning and root architectural differences between and within species and sites. This chapter is intended to explain the responses observed in Chapter 2 and 3, where different degrees of soil water depletion and xylem water potential were observed for both species and study sites. This information can be used to support management decisions to effectively and efficiently control weed species, such as Senecio, that compete with crop trees, such as Douglas-fir**.** This study hypothesizes that i) under reduced soil water availability, Senecio will have increased allocation to belowground components while Douglas-fir is less responsive , ii) more aggressive growth of Senecio's root system will be reflected in wider root length and greater number of root tips, and iii) simple visual observations of Senecio cover and height can be used to estimate Senecio biomass per unit ground area.

Methods

Site Selection

Study sites were located in newly planted Douglas-fir plantations in areas expected to have high amounts of Senecio. After consulting with VMRC cooperators, three study sites were selected in order to capture a gradient of site conditions across western Oregon. All of the selected sites received a pre-planting fall site preparation herbicide application (FSP); within each site, a uniform 0.3 ha (61 x 61 m) study area was identified and excluded from any further herbicide application. By excluding these areas from any post-planting spring release treatments, a large amount of Senecio was expected at each site.

The first site is managed by Cascade Timber Consulting Inc. and is situated on a plateau near a steep slope overlooking the town of Sweet Home (SH, Figure 1, Figure 2a). This study site is located at 44°22'00.9"N 122°42'29.7"W in the central Cascade Range of Oregon at approximately 320 m above sea level and 109 km East of the Pacific Ocean. The site has a mean annual temperature of 10.8°C, mean annual precipitation of 1705 mm, and soils in the Peavine and Kilchis-Harrington series defined as silty clay loam with stony loam (Wang et al., 2012; Soil Survey Staff, 2019). Observations also indicate that the soil has some areas that contained significant gravel and coarse material, including decomposing cedar. This site had the highest average soil clay content (36%), the lowest sand content (30%), the highest field capacity (0.39 cm^3 cm^{-3}), and lowest available soil water (ASW; 0.14 cm^3 cm^{-3}) of the three sites. This was our intermediate site, as it was neither extreme in temperature nor relative humidity. The site was planted with bareroot plug+1 Douglas-fir seedlings. The tank mix used in FSP included 2 qts. of glyphosate, 16 oz. of imazapyr, 4 oz. of Oust Extra and 8 oz. of MSO.

The second site is managed by the Oregon Department of Forestry and is located on a steep SE facing slope near Burnt Woods, OR (BW, Figure 1, Figure 2b). This study site is located at 44°35'14.2"N 123°40'57.0"W in the Coastal Range and is approximately 410 m above sea level and 35 km from Pacific Ocean. The site received a broadcast prescribed burn before planting, has a mean annual temperature of 10.2℃, mean annual precipitation of 2075 mm, and soils in the Preacher-Bohannon-Slickrock complex (Wang et al., 2012; Soil Survey Staff, 2019). This soil texture consists of loam weathered from sedimentary rock types, loam from sandstone, and Slickrock gravelly loam. Over the sampling period, this site received the most rainfall. This site also had the highest average soil sand percentage (36%), lowest clay content (30%), and greatest ASW (0.16 cm^3 cm^{-3}) of the three sites. The site was planted with styro 20 containerized Douglas-fir seedlings. The tank mix used in FSP included 2 qts. of glyphosate and 4 oz. of Oust Extra.

The third site is owned by Roseburg Forest Products Inc. and is located near Veneta, OR (VN, Figure 1, Figure 2c). This study site is located at 43°56'25.3"N 123°23'58.3"W in the south-central valley and is approximately 266 m above sea level and is 65 km from the Pacific Ocean. It has a mean annual temperature of 11℃, mean annual precipitation of 1422 mm, and soils in the Peavine series defined as a silty clay loam (Wang et al., 2012; Soil Survey Staff, 2019). This site had the highest average soil silt content (38%), and the lowest wilting point (0.22 cm^3 cm^{-3}). This was our dry site and it also had the most extreme weather conditions: highest temperatures, lowest relative humidity (highest VPD), and the least amount of rain. The site was planted with bareroot plug+1 Douglas-fir seedlings. The tank mix used in FSP included 2.25 qts. of glyphosate 5.4, 4 oz. of Oust XP and 1 oz. of MSM 60.

Senecio Cover and Biomass Dynamics

As previously shown in Chapters 2 and 3, assessments of Senecio cover and height were carried out at every soil moisture probe location (n=8) and sampled tree (n=16) at each site every two to three weeks during the growing season of 2019 (between May and late September). Vegetation cover and height were estimated visually at each location using a 1x1 m square. If the cover of non-Senecio species was greater than 5% in any vegetation survey area, or the areas surrounding the tree seedlings, that non-Senecio vegetation was removed by hand. Additionally, at each site, three clip plots with an area of 1 m^2 were sampled monthly during the sampling period to develop equations to convert Senecio cover percent and height (% m) to biomass (Mg ha^{-1}). The cover and height of Senecio in these clip plots was first estimated visually before cutting all the live above-ground biomass. All Senecio material from each clip plot was put into paper bags and dried at the VMRC lab for 72 hours at 65°C before being weighed. Clip plot locations were systematically selected to represent the range of Senecio abundance (from 0% to highest cover % observed) found across the study area at each of the three sites. A linear model was used to describe the relationship between Senecio biomass and cover %:

$$\mathrm{SB} = \mathrm{a} + \mathrm{b}^{*}\mathrm{CxH} \tag{2}$$

where SB is the aboveground biomass of Senecio (Mg ha^{-1}), C is the percent cover of Senecio (%), H is Senecio height (cm) and a and b are linear regression parameters.

In order to quantify individual plant allometry, 10 complete Senecio and Douglas-fir individuals at each site were excavated and taken back to the lab for morphology and biomass measurements. Photos were taken of each fresh sample's root system and used to take measures of root volume and number of root tips using WinRHIZO image analysis system (WinRHIZO Pro, Regent Instruments, Quebec, Canada). Measurements were taken of the total height (H, cm), the number of root tips (NTips), longest vertical root length (VRL, cm), and two horizontal root lengths (HRL, cm). The HRL included the longest horizontal root length and the longest horizontal root on the opposite side of the root system. The root volume (RV, cm^3) of each individual was measured using the water displacement method. After that, all plants were oven-dried at 65ºC for 72 hours and weighed to get aboveground (AGB, g) and belowground (BGB, g) dry mass. The relationship between individual height and biomass of Senecio plants was assessed using an exponential model:

$$\mathrm{Bi} = \mathrm{a} \cdot \mathrm{e}^{\mathrm{b} \cdot \mathrm{H}} \tag{3}$$

where Bi is the individual Senecio plant dry mass (above or below ground, g), H is the height of the individual Senecio plant (cm), and a and b are curve fit parameters.

For Douglas-fir biomass, a linear model was a better fit:

$$\mathrm{BiDF}=\mathrm{a}+\mathrm{b}*\mathrm{x}$$

where BiDF is the individual Douglas-fir seedling dry mass (above or below ground, g), H is the height of the individual Douglas-fir seedling (cm), and a and b are curve fit parameters.

For Senecio root dimensions, a linear model was the best fit:

$$\mathrm{BiSESY}=\mathrm{a}+\mathrm{b}*\mathrm{x}$$

where BiSESY is the individual Senecio root dimension (HRL, VRL, cm), H is the height of the individual plant (cm), and a and b are curve fit parameters.

Using HRL data, the area of influence for root absorption (AI, cm^2) was estimated for each sampled Douglas-fir and Senecio plant using the following equation:

$$\mathrm{AI} = \pi \cdot \left(\frac{\mathrm{HRL}}{2}\right)^2 \tag{4}$$

where AI is the area of influence for root absorption (cm^2) and HRL is the horizontal root length (cm).

Statistical Analysis

Analyses were done using SAS version 9.4 (2020) for model building and statistical tests (PROC GLM and PROC NLIN). Linear regression models were used to correlate Senecio cover by height and Biomass; Douglas-fir belowground biomass, aboveground biomass, and Senecio root horizontal length and root vertical length. Model fitting was done using SAS for Senecio aboveground and belowground biomass. Two-Way Analyses of Variance (ANOVA) with Tukey Post-Hoc tests were used to determine the effect of species, site, and the interaction of species by site. Results are shown in Table 1 and Appendix Table 1. All significance tests used $\alpha = 0.05$. Sigmaplot version 14 (Systat Software, Inc. San Jose, CA, USA) was used to make all figures.

Results and Discussion

Weather Conditions

Weather stations collected data at SH and VN beginning in mid-April. Our original third site was moved in May when little to no Senecio abundance was observed; for BW, therefore, measurements began in late May. There were differences between sites for the weekly mean weather variables from April to late September (Figure 1). The VN site had the highest temperatures, lowest relative humidity and least amount of rainfall, with little-to-no rain from June 1st until the beginning of September. The SH and BW sites both had more precipitation events, especially in June which recharged the soil and helped to reduce the length and intensity of the seasonal drought. Over the shared measurement period (5/31-9/27), the VN site had 62 mm of rain, while the SH and BW sites had 227 mm and 171 mm of rainfall, respectively. The mean growing season temperature for VN, SH and BW sites was 16.8, 16.1, and 16.2 ºC, respectively. The mean RH was 72, 75 and 81% for the VN, SH and BW sites, respectively. This data reflects that drought conditions were most intense at the VN site compared to the SH or BW sites.

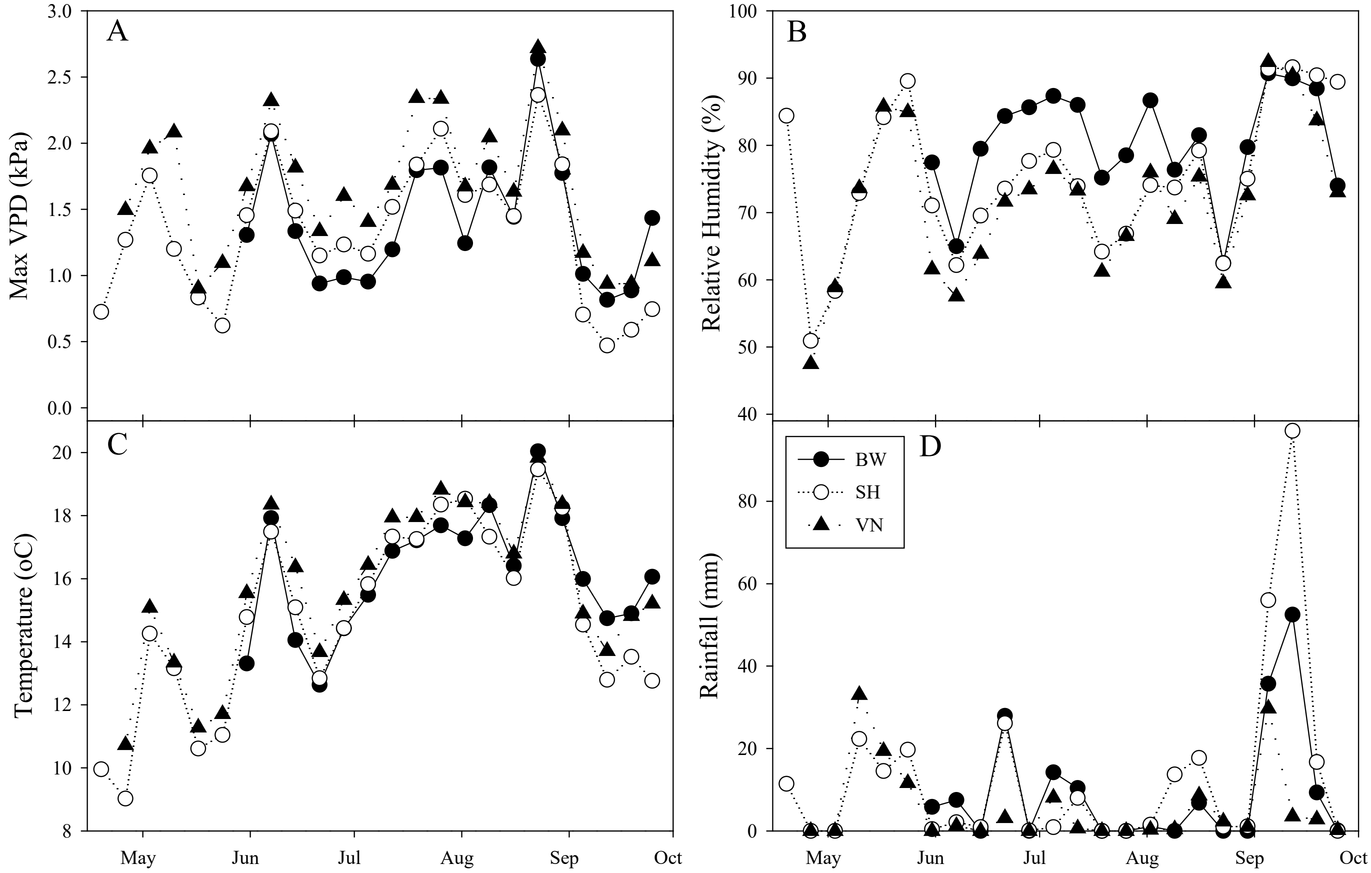

Figure 1. Weekly mean: A) maximum VPD, B) relative humidity, C) air temperature and D) total rainfall, for the BW (filled circle), SH (open circle) and VN (filled triangle) sites.

Senecio Biomass per Unit Ground Area

There was a strong relationship ($P<0.001$, $R^2=0.93$) between Cover% by Height (% m) and aboveground biomass (Mg ha^{-1}) of Senecio (Figure 2) which was shared across sites. Other studies have also shown good correlations between vegetation cover, height, and biomass (Evans and Jones, 1958; Matilla, 1981; Kuusipalo, 1983; Axmanova et al., 2012). Overall, 1.7 Mg ha^{-1} of Senecio is predicted to be on sites with a CxH of 20 % m. On sites with CxH of 100 % m, the aboveground biomass of Senecio should be 8 Mg ha^{-1}. The BW site had the greatest cover by height values, which explains the highest sampled biomass values observed at the site, almost up to 11 Mg ha^{-1} (Figure 2). Parameter estimates and curve fit statistics are shown in Appendix Table 1.

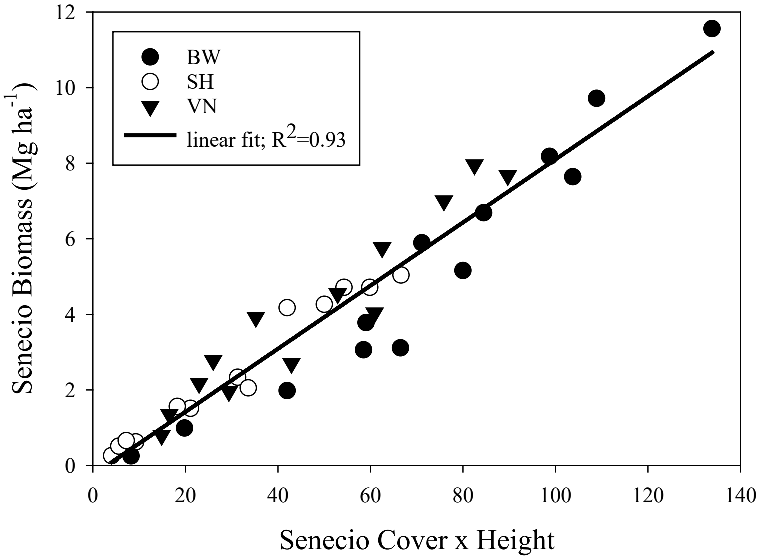

Figure 2. Relationship between cover x height (% m) and aboveground biomass (Mg ha^{-1}) for Senecio growing at the BW (filled circle), SH (open circle) and VN (filled triangle) sites.

Senecio Biomass Seasonal Dynamics

Each site had vegetation surveys done at all 8 probes every two to three weeks (see Chapters 2 and 3). Cover and height were transformed into biomass using the function from Figure 2. The site-specific seasonal abundance dynamics of Senecio at BW and VN, for instance, can be described as undergoing a quick early successional peak and a plateauing period followed by senescence and loss of biomass after florescence. SH had a different pattern of gradual colonization followed by slower senescence; there was also the germination of a second generation of Senecio which prolonged local water depletion and biomass values. BW had the tallest Senecio, and its residual presence at the site in August is the product of some loss of cover percent but no loss in height. BW had the highest levels of biomass over the growing season, followed by VN, then SH, whose abundance values never matched those of the other two sites.

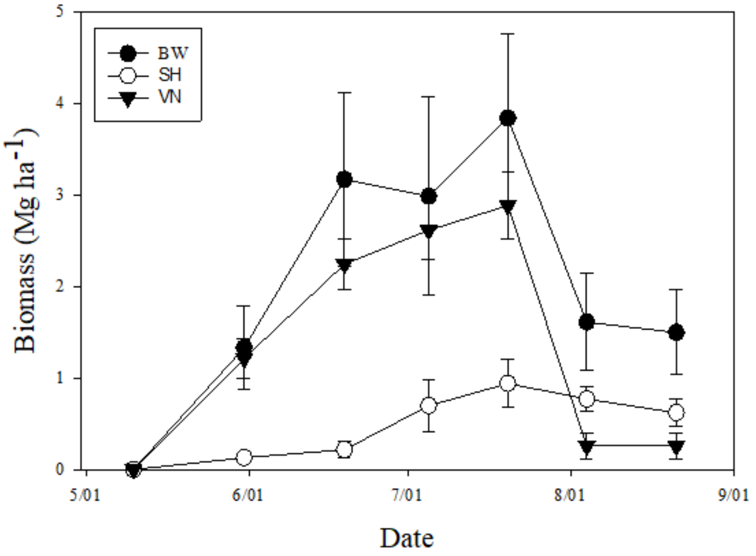

Figure 3. Seasonal dynamics of aboveground biomass (Mg ha^{-1}) of Senecio growing at the BW (filled circle), SH (open circle) and VN (filled triangle) sites.

Senecio and Douglas-fir Biomass Partitioning and Root Architecture

For individual Senecio plants, the relationship between height (H) and dry mass for both Above Ground Biomass (AGB) and Below Ground Biomass (BGB) was different across the three sites (Figure 4). For instance, Senecio growing at the SH site had higher biomass for any given unit of height than the other two sites ($P<0.0001$) (Figure 4b and 4d). For Douglas-fir (Figure 4 a and c), there were no significant differences between sites ($P=0.32$). The relationship between H and biomass was different between species ($P=0.0076$ for AGB; $P<0.0001$ for BGB). The slopes of the responses were also different: for Senecio, the AGB and BGB were exponentially related to H; for Douglas-fir, there was a linear relationship. As such, any increase in Senecio H is associated with a greater increase in biomass compared to Douglas-fir. This difference in allometry could be the effect of differences in population density (larger cover% at the BW site, lower cover% at the SH site) that may have affected the height to biomass relationship. Parameter estimates and model fit statistics are shown in Appendix table 1.

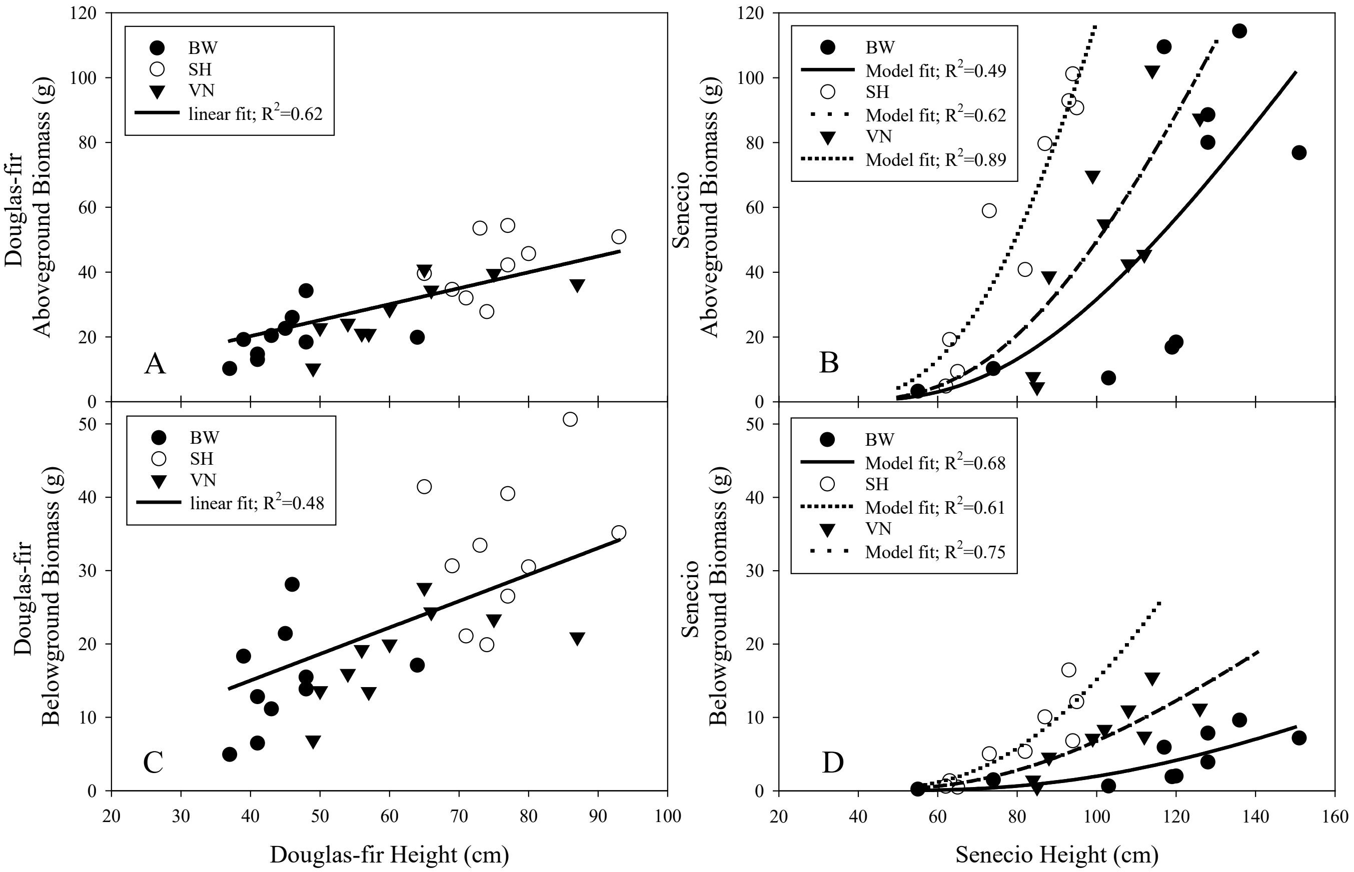

Figure 4. Relationship between height (H, cm) and aboveground (A, B) and belowground (C, D) biomass for Douglas-fir (left) and Senecio (right) plants growing at BW (filled circle), SH (open circle) and VN (filled triangle) sites. For Douglas-fir, curve fit is depicted as solid black line. For Senecio, curve fit is depicted as solid black line (BW), dashed black line (SH) and solid gray line (VN).

The fact that the site-specific relationships between Senecio H and biomass and root length held true illustrates the polymorphic flexibility of an invasive species like Senecio that allows it to respond to cues from the local environment and exploit disturbed sites (Ernst, 1985). The differences between sites illustrates that there are not strictly programmed differences between the species, but that Senecio is tailoring its allocation patterns based on environmental cues while Douglas-fir is not nearly as responsive. This plastic quality of invasive species like Senecio has been shown in other work as well (e.g. Davidson et al., 2011). At SH, the steeper relationship between height and biomass could be the result of the favorable conditions at the site: lower overall

Senecio % cover, and therefore less competition for resources, as well as the most rainfall over the sampling period (227 mm) compared to the other sites (62 mm at VN; 171 mm at BW). The fact that BW had the lowest response values of the three sites could be because of the intense amount of competition shown in Chapter 2: BW had the highest overall height, cover percent, and biomass. It is therefore consistent with the literature that BW would have individuals with lower biomass and root lengths for any given unit of height, as they must emphasize height growth to get access to light (Pan et al., 2013).

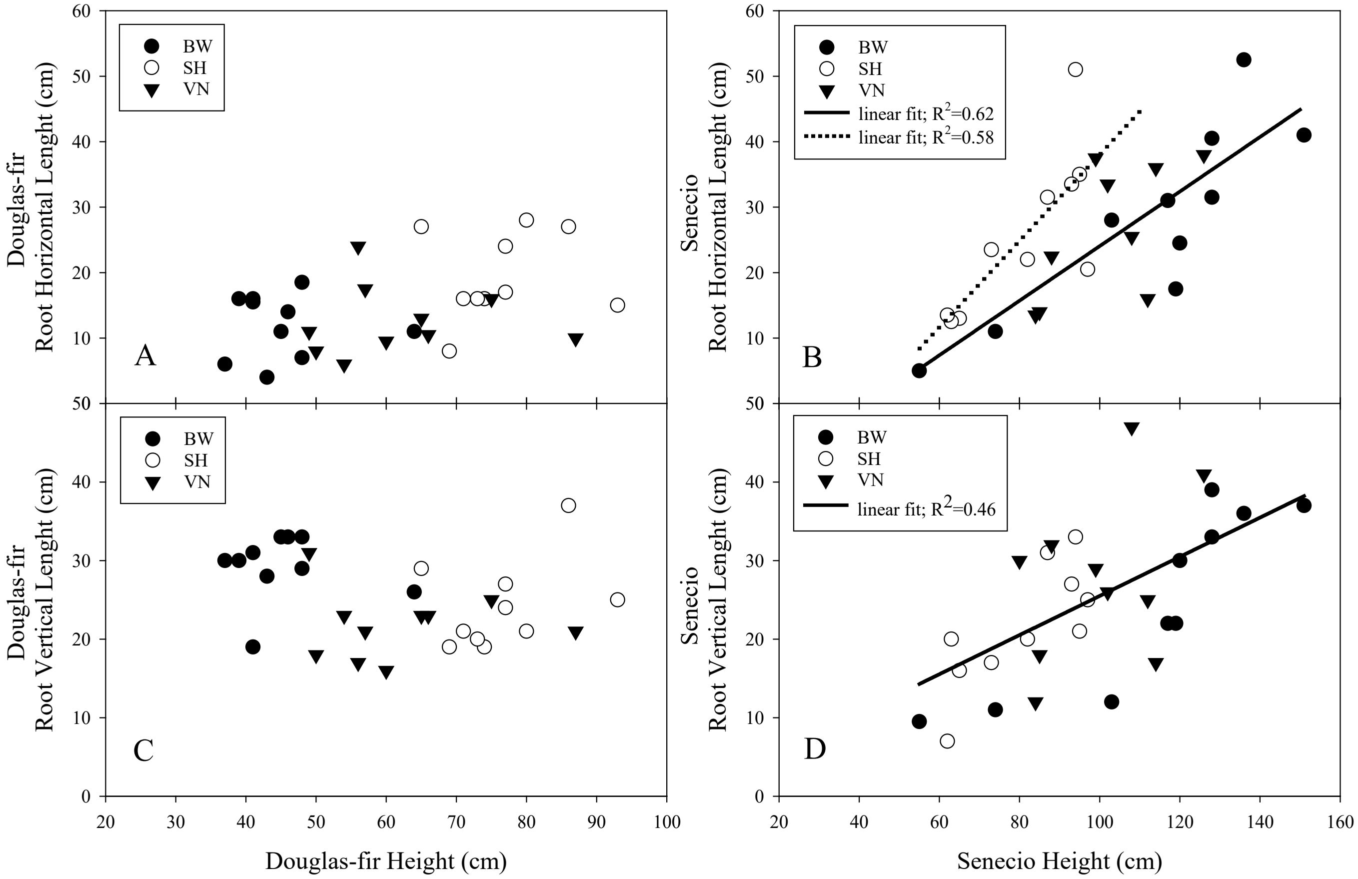

Figure 5. Relationship between height (H, cm) and horizonal (RHL, A, B) and vertical (RVL, C, D) root lenght for Douglas-fir (left) and Senecio (right) plants growing at BW (filled circle), SH (open circle) and VN (filled triangle) sites. For Douglas-fir, curve fit was not significant. For Senecio, curve fit for RHL is depicted as solid black line for WB and VN sites, and as dashed line for SH site; curve fit for RVL is depicted as solid line.

Figure 5 shows the interspecies differences for responses of root architecture to increases in plant H: Douglas-fir root dimensions were independent of H increases, while Senecio root dimensions increased in response to H. For Douglas-fir, the lack of a relationship between H and root length was likely the result of the stock type from the nursery (bareroot P+1 at SH and VN; styro plug 20 at BH site) rather than growth during the growing season.

It is worth noting that although Douglas-fir had on average more belowground biomass, the RHL was significantly lower than that of Senecio ($P<0.0001$; Table 1). For Senecio, SH was once again different from the other sites ($P<0.0001$) for RHL, as it was more responsive to any given increase in height. For RHL, the average of Senecio was larger: Douglas-fir average RHL was 14.6 cm; Senecio average RHL was 29.3 cm ($P<0.0001$, Table 1). On the other hand, RVL was not significantly different across species or sites ($P=0.78$, Table 1), averaging 25.1 and 24.5 cm for Douglas-fir and Senecio, respectively. This result may explain the differences in water stress shown in Chapter 3. Even though Douglas-fir and Senecio were accessing soil water at the same soil depth, Senecio increased its exploitive root zone horizontally, while Douglas-fir was relatively limited in this capacity.

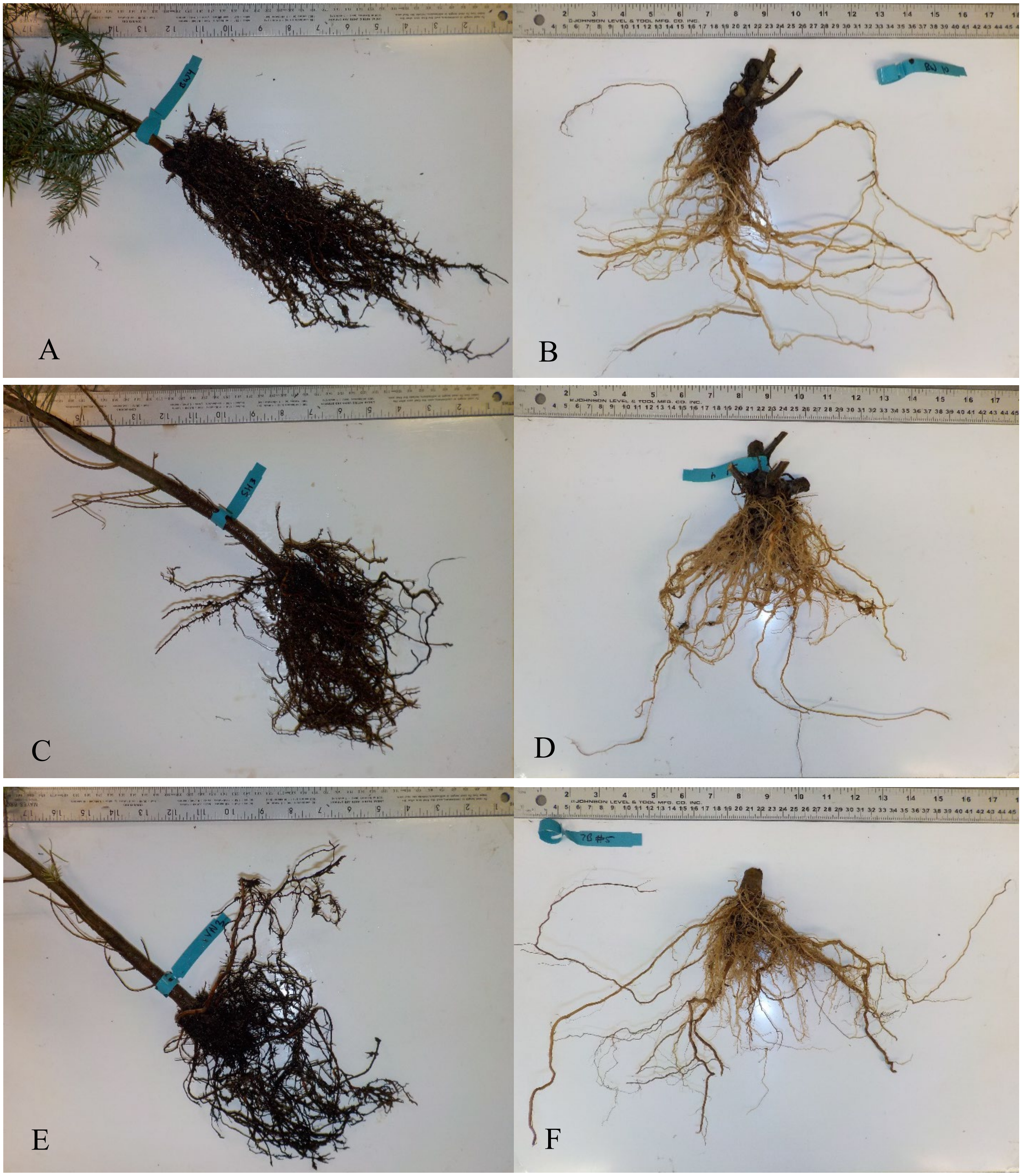

Figure 6. Example images of root system for Douglas-fir (left) and Senecio (right) growing at the BW (upper panel), SH (middle panel) and VN (lower panel) sites.

There are distinctly different root architectural forms of Senecio and Douglas-fir across sites. The images in Figure 6 typify the general species-wide trend seen at these sites: the Douglas-fir grew dense matted roots in a limited area, which increased the biomass values over Senecio, but it had about half the root zone area of influence (AI, Table 1). Senecio, on the other hand, had fewer clusters of roots and instead preferentially grew roots horizontally, likely in direct response to available soil water. This efficient allocation of biomass and resources could explain why Senecio had overall less water stress as seen in Chapter 3.

Table 1 shows mean values and P-values from a two-way ANOVA for biomass and root architecture measured for Douglas-fir and Senecio at the three study sites. There were significant interactions between species and site for BGB, shoot:root and NTips (P=0.0015, 0.0306 and 0.066, respectively), implying that differences across sites depended on the species. For example, Douglas-fir seedlings growing at the SH site had two times more BGB than those growing at the BW site (P<0.0001), while BGB of Senecio plants was not different across sites (P=0.37).

Table 1 also shows the different allocation patterns towards fine roots tips for each species across the different sites. Although the number of tips for all other size categories >0.5 mm were not significantly different, there were distinct differences in the number of fine root tips (<0.5 mm) that were produced (P=0.066). Senecio at VN had the highest overall number of fine tips, which is expected given water was limiting at this site. It is interesting, however, that Douglas-fir at VN had the fewest number of fine tips; this could be because of the response Jansen et al. (2014) noted, where under intense drought stress more energy is put into coarse root development and exploration than fine roots. Furthermore, Kramer and Boyer (1995) discuss the general trend of plants responding to dry soils by emphasizing root growth over shoot growth; in many cases, it is the extension of coarse roots into unexploited horizontal or vertical zones of water availability that pays back this investment (e.g. Klepper 1973; Gales, 1979; Malik et at., 1979; Stewart and Nielsen, 1990). Therefore, VN Douglas-fir was potentially putting more energy into existing roots instead of developing new fine root tips that explore soil that is already nearly depleted of FASW as early as June 14th by Senecio (Chapter 2).

As seen in Table 1, the Senecio shoot:root ratio was the highest at BW for the three sites. This difference was significant compared to VN (P=0.0091), and nearly so compared to SH (P=0.087); this is likely due to the intense amount of intraspecific competition. This competition prompted the individual plants to favor aboveground biomass and height over belowground biomass likely in response to light competition, which is significantly more limiting than water competition (Drever et al., 2001). This intraspecific responsivity is supported by research such as Abbott (1976) who found that there was a large degree of variation for biomass partitioning of Senecio across habitats in response to differing amounts of moisture, wind, and nutrient stress; West and Chilcote (1968) also found similar sensitivities to intraspecific competition. Work by Van Andel and Dueck (1982) supports this as well, as the authors found that *Senecio vulgaris, viscosus,* and *sylvaticus* growing at fixed distances from one another had 250% greater seed production compared to those grown in clusters. The results at BW, where the shoot:root ratio was the highest of the three sites, is consistent with these results as well.

Table 1. Mean values of aboveground biomass (AGB, g), belowground biomass (BGB, g), shoot to root ratio (shoot:root, g g^{-1}), number of root tips (NTips), root volume (RV, cm^3), root horizontal length (RHL, cm), root vertical length (RVL, cm) and area of influence for water extraction (AI, cm^2) for Douglas-fir seedlings and individual Senecio plants growing at the BW, SH and VN sites in Central Oregon.

Species	Site	AGB	BGB	shoot:root	NTips	RV	RHL	RVL	AI
	Site	g	g	g g^{-1}		cm^3	cm	cm	m^2
Douglas-fir	BW	19.9	14.9	1.51	625	16.1	11.9	29.2	241.7
	SH	46.9	31.0	1.62	677	16.2	19.4	24.2	512.2
	VN	27.9	18.5	1.51	428	13.4	12.6	21.8	268.7
Senecio	BW	52.6	4.1	12.41	714	25.3	29.4	24.15	620.8
	SH	51.3	6.0	10.61	852	30.5	28.0	21.7	774.9
	VN	53.6	7.5	7.65	1053	35.0	30.6	27.7	639.9
ANOVA	Factor								
P>F*	Site	0.3712	0.0004	0.0296	0.716	0.760	0.653	0.3199	0.9712
	Species	0.0076	<.0001	<.0001	0.004	0.0004	<.0001	0.7837	<.0001
	Site*Species	0.2853	0.0015	0.0306	0.066	0.449	0.299	0.0727	0.7576

Table 1 shows that there was a significant difference between species for the RHL ($P<0.0001$). The lack of Douglas-fir seedling root expansion could be partly explained by transplant shock factors such as injury to roots, loss of fine roots, and disconnection from the previously established soil contact points (Kozlowski, 2002). Competition with Senecio at the two sites with the greatest abundance (BW and VN) could have exacerbated any of these factors, while the SH Douglas-fir could have had resources available to recover and achieve greater growth gains for both aboveground and belowground biomass compared to the other sites.

These results could show that the minimal water stress that Senecio was experiencing over the entire growing season, even at the driest site, was the result of efficient and responsive root biomass and dimensional allocation to exploit available soil water. This would not be surprising, given that Eziz et al. (2017) showed that for annual herbaceous plants, such as Senecio, the Root Mass Fraction (RMF) was increased much more (10% v/s 5.5%) in response to drought than woody-stemmed or perennial herbs. The results shown here illustrate that Senecio increased its RMF by 39% from the wettest (SH) to the driest (VN) site; the Douglas-fir allocation shift from SH to VN was a 7% increase in RMF, which is much closer to the expected 5.5% shown in Eziz et al (2017). The large differentiation between these two species' allocation patterns could illustrate Senecio's plastic life history traits favoring responsive expansion which can prime it for efficient exploitation in many different environments.

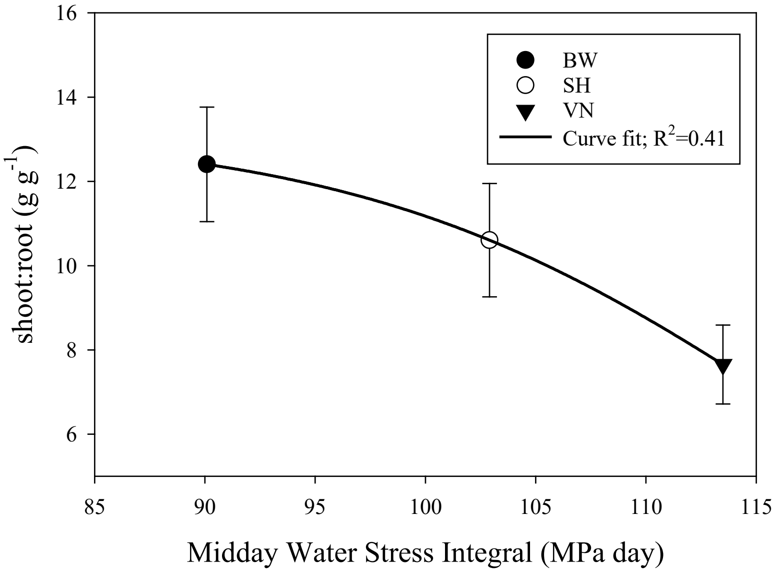

Figure 7. Relationship between midday water stress integral (reported in Chapter 3) and shoot to root ratio (g g^{-1}) for Senecio plants growing at the BW (filled circle), SH (open circle) and VN (filled triangle) sites. A sigmoidal curve showed the best fit for the data.

There is a clear relationship between midday water stress integral (WSI_{MD}, MPa day) measured at the end of the growing season and shoot:root ratio of Senecio across the three study sites. These results demonstrate that as the cumulative seasonal water stress increases (WSI_{MD}), the shoot:root ratio decreases. Poorter et al. (2012) support this, noting that drought stress is associated with decreased Leaf Mass Fraction (LMF) and Stem Mass (SMF) Fraction, while Root Mass Fraction (RMF) increases. This is also supported by work such as Chan et al. (2003) who found that when water was a limiting factor more energy was allocated to roots. The results here illustrate Senecio's larger phenotypic plasticity, which preferentially allocates biomass to the limiting resource; this allocation proportion shift is much greater for Senecio (12.5 for BW, 11 for SH, and 8 for VN) than for Douglas-fir, whose shoot to root ratios were similar across sites: 1.62 for SH, 1.51 for VN, and 1.51 for BW. This analysis was possible for Senecio because it grew from seed to apical form then senesced; for Douglas-fir, we were not able to obtain initial measurements because the seedlings were grown at the nursery before out-planting. This precludes the possibility of getting access to the initial root size values for biomass, volume, and length and associating them with the change in WSI over time.

Overall, the Senecio across all sites had approximately 2 times the horizontal area of influence per individual plant compared to the Douglas-fir; these differences were significant: $P<0.0001$ (Table 1). The Douglas-fir at SH brought up the average area of root influence compared to BW and VN, where the difference was even more pronounced (Table 1); excluding SH would make the average area of influence for Douglas-fir only 255 cm^2, which makes it 2.7 times smaller than Senecio's average root zone of influence. This is an important illustration of how even at an individual level Senecio intensively occupies a site. Furthermore, Senecio has been noted to inhabit sites at a density of 22 individuals per m^2 (Dinger et al., 2012), which will further increase the competition for resources between Douglas-fir and Senecio. Because of Senecio's responsivity to limiting resource conditions compared to Douglas-fir, this high individual capacity for exploitation of resources combined with a high density of colonization will likely increase drought stress and induce growth losses for the Douglas-fir.

Senecio's general root architecture illustrates a distinct pattern of horizontal exploitation by extending primary coarse roots up to 30 cm on average (Table 1) from the stem; the Douglas-fir, however, grew a greater number of denser matted roots in a smaller area. The Senecio is therefore avoiding competition with its own roots and increasing the exploitive efficiency of the roots it invests in. This is consistent with Kramer and Boyer's (1995) position that decreasing the uptake per unit of root surface detracts from the benefits of increased root length density. As Turner and Kramer (1980) note, plant emphasis on root area over root density is key for increasing access to water in dry soils, as the total exploitable area vastly increases with the former allocation.

Senecio showed this trend by increasing its area of influence through coarse root horizontal expansion, as well as fine root development (number of fine tips), putting more energy into expanding access to water instead of increasing the root volume or biomass in a smaller area like the Douglas-fir. All these results illustrate that there are distinct differences between the allocation patterns of Senecio and Douglas-fir; the former shows a much greater responsivity to site conditions compared to the latter. Management decisions should therefore take into consideration the life history traits of Senecio shown here to better optimize Douglas-fir growth patterns, especially in the context of site conditions and changing climate trends.

Conclusions

In this study we examined the allocation patterns of Senecio and Douglas-fir. These patterns are likely responses to varying climatic factors, soil conditions, and vegetation abundance; however, the degree of response differed significantly between species for many traits (Table 1). This was most pronounced for the shoot:root ratio, the total amount of below-ground biomass, and the associated root dimensions. At the dry site, both Douglas-fir and Senecio showed a preferential effect on allocation, although this effect was much greater for Senecio than Douglas-fir (39% greater dry-site response difference in root allocation for Senecio vs 7% for Douglas-fir). Although BW had more moisture than VN, it also had more competition, and this resulted in Senecio prioritizing height and stem biomass over root biomass. This increased competition also could be responsible for the lack of Douglas-fir horizontal expansion seen at BW. Senecio had on average twice the root area of influence compared to Douglas-fir across sites. Overall these results illustrate the high exploitive efficiency of Senecio and its plastic phenotypic potential to respond to varied site conditions. Douglas-fir, on the other hand, was much less pronounced in its reaction to site conditions. This likely has stand growth consequences given the projected decreases in rainfall, increases in temperature which exacerbates evaporative demand, and the increased frequency of heat waves. Because of the different responses between species, management regimes need to consider the likely impact of Senecio, especially at dry sites such as shown in VN.

Appendix:

Site	Trait	Model	Parameter	Parameter Estimate	R^2	RMSE
SESY:BW	AGB	IS-AGB= a*exp(b/x)	*a*	1042.7163	0.489	34.28
			b	-349.3984		
	BGB	*	*a*	165.2581	0.610	2.22
			b	-441.8833		
	RHL	IS-HRL=a + b*x	*a*	-17.6357	0.617	7.87
			b	0.4168		
	RVL	**	*a*	.5640	0.432	7.57
			b	.2490		
SESY:SH	AGB	*	*a*	3181.5066	0.892	13.34
			b	-329.7771		
	BGB	*	*a*	707.9100	0.754	2.93
			b	-384.2138		
	RHL	**	*a*	-27.8518	0.581	8.41
			b	0.6591		
	RVL	**	*a*	.5640	0.432	7.57
			b	.2490		
SESY:VN	AGB	*	*a*	1631.6202	0.623	21.54
			b	-357.9458		
	BGB	*	*a*	234.9890	0.678	2.92
			b	-354.1661		
	RHL	**	*a*	-17.6357	0.617	7.87
			b	0.4168		
	RVL	**	*a*	.5640	0.432	7.57
			b	.2490		
DF	AGB	IS-AGB=a+b*x	*a*	.5640	0.624	7.72
			b	.4930		
DF	BGB	***	*a*	.5640	0.479	7.81
			b	.3610		
	SB	SB= a+b*SC	*a*	-0.0387	0.3213	0.930
			b	0.0757	0.0063	

Table A1. Parameter estimates and model fit statistics for the *S. sylvaticus* allometry.

IS-AGB: Individual Senecio plant aboveground biomass (g); IS-BGB: Individual Senecio plant belowground biomass (g); IS-RVOL: individual Senecio plant root volume (cm3); IS-HRL: individual Senecio plant horizontal root length (cm); IS-RVL: individual Senecio vertical root length (cm); HT: Individual Senecio plant height (cm); BW: Burnt woods site; SC: Senecio cover (%); ASB: where SB is the biomass of Senecio (Mg ha^{-1}) at the site. SE: standard error; R^2: coefficient of determination. For all parameter estimates: $P < 0.05$.

* IS-Biomass= a*exp(b/x)

** IS-RootLength=a + b*x

***IS-Biomass=a+b*x

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Chapter 5: Conclusions

Summary of Findings

In this study we showed that the hypotheses outlined in Chapter 1 were supported by our results. In Chapter 2, we illustrated that a greater abundance (cover % and height) of Senecio was correlated with increased soil moisture depletion. Specifically, those areas with a greater % cover of Senecio around them showed increased local soil water depletion; this occurred to a greater degree at the dry site (VN) compared to the other wetter sites (SH and BW).

For Chapter 3, we showed that lower site water levels induced competition between Douglas-fir seedlings and Senecio which increased water stress in Douglas-fir seedlings to varying degrees across different environments. Those seedlings with higher abundances of Senecio around them showed increased local soil water depletion and had more negative predawn and midday water potential values. This effect was once again most pronounced at the dry site (VN) compared to the two wetter sites (SH and BW), although this effect varied between sites over time.

For Chapter 4, we showed that in response to limiting soil moisture, Senecio increased its proportional allocation to belowground components. Compared to the Douglas-fir, Senecio had increased horizontal root length, but the vertical root lengths were very similar. This chapter showed that simple visual observations of Senecio cover and height can be used to estimate Senecio biomass per unit ground area. In general, Senecio was much more responsive to changing site conditions than was Douglas-fir.

Overview of Results

The goal of the research presented in this thesis was to quantify the effects of early seral competition by Senecio on Douglas-fir tree seedling water stress using predawn and midday water potential assessments across a range of sites in Western Oregon. This information can be used to support management decisions to effectively and efficiently control weed species, such as Senecio, that compete with crop trees.

Chapter 2 showed that soil moisture probes surrounded by higher levels of Senecio had much higher rates of soil water depletion than those with less cover demonstrating the competitiveness and rapid resource utilization of Senecio. For VN, the dry site, this occurred earliest and to the greatest degree in July; for BW, this occurred during August; for SH, our wettest site, the greatest correlation between Senecio cover and depletion was in early September. Furthermore, fractional available soil water was reduced to 35% from 65% in August with a Senecio cover of only 20% at SH. This effect was greater at SH but also similar to the other two sites.

Chapter 3 showed the effects of Senecio on drought stress inducement across sites with varying climate, soil, and Senecio abundance conditions. The degree of Senecio abundance on Douglas-fir drought stress was more pronounced at each site only during periods when FASW was depleted. For VN, the dry site, this occurred earliest and to the greatest degree in July, while the other sites weren't depleted of water until later in August and September. Our results show that a greater abundance of Senecio translated to faster soil moisture depletion and more negative xylem water potential for both Ψ_{PD} and Ψ_{MD} of Douglas-fir seedlings. However, the degree of this impact differed across sites and over time, largely because of the atmospheric and soil conditions at the sites. The impacts of Senecio presence and water depletion were most severe in the dry (higher water deficit) site than the wet sites, which extended the drought season and induced intense water stress in Douglas-fir seedlings.

Chapter 4 examined the allocation patterns of Senecio and Douglas-fir. These patterns are likely responses to varying climate, soil conditions, and vegetation abundance; however, the degree of response differed significantly between species for many traits. This was most pronounced for the shoot:root ratio, the total amount of below-ground biomass, and the associated root dimensions. At the dry site, both Douglas-fir and Senecio showed a preferential effect on allocation, although this effect was much greater for Senecio than Douglas-fir (39% greater dry-site response difference in root allocation for Senecio vs 7% for Douglas-fir).

Management Implications

This study has shown that not all abundances of Senecio have the same impact on Douglas-fir; the incredibly high biomass values shown at BW (nearly 12 Mg ha^{-1}), for instance, did not correspond to the highest levels of Ψ_{PD} seen in Chapter 3. The biomass function, in association with weather, soil moisture data-including average depletion by Senecio seen in Chapter 2-, and the allometric results presented here, can be used to evaluate the likely impact of Senecio on water resources and Douglas-fir drought stress and allometric pathways. The results from this study can help to inform management decisions on a site-specific context when deciding on the appropriate amount of control and tolerated abundance of competing vegetation. Overall, this study showed that Senecio presence is more deleterious and impactful at dry sites where water is a limiting resource than at wetter sites. Even at this dry site the Senecio did not show any significant elevation of water stress over its entire lifespan compared to the other sites where much more water was available. This shows that the plastic quality of Senecio necessitates control measures that limit the continued reproduction and spread of this invasive species. This depletion of soil water and inducement of Douglas-fir drought stress can be mitigated operationally by prioritizing a spring release treatment at sites which have been, or are at risk of, being invaded by high abundances of Senecio. This buffering against water stress and concomitant stomatal conductance losses can likely improve growth gains of the Douglas-fir and help optimize volume production and the timing of harvest.

Future Directions

The information from this study can be developed further in many areas, from industry to research. For example, the association of Senecio cover % and water depletion as a function of site conditions such as weather and soil qualities can be used to build a Senecio water use model with relatively simple inputs. The results presented here also can be used in forest planning operations by accounting for the likely impact of Senecio, especially its pronounced impact in sites where moisture is limiting. The different allocation pathways of competing vegetation and desired crop trees also deserves more study, especially in response to changing climate conditions in order to ensure the establishment and optimal growth trajectories of the desired Douglas-fir crop tree seedlings.