The Influence of Site Conditions on *Senecio sylvaticus* Seasonal Abundance, Soil Moisture Dynamics, and Douglas-fir Seedling Water Stress

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Abstract

Competition for soil water resources between newly planted Douglas-fir seedlings and aggressive early-seral plants, such as *Senecio sylvaticus* [L.] (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 varying site conditions has not been quantified. This study quantified these interactions at three contrasting sites across the U.S. Pacific Northwest: the Coastal Range, the Cascade foothills, and the fringe of south-central valley of Western Oregon. We tested whether competition between Senecio and Douglas-fir seedlings for soil water resources in areas of high Senecio abundance caused increased water stress in the tree seedlings. Senecio demonstrated a high degree of plasticity across sites increasing its lifespan and shoot:root in response to increased soil water resources. Senecio also had more than twice the root area of influence as Douglas-fir. Overall, greater Senecio abundance was associated with greater soil moisture depletion and this soil moisture depletion was correlated with increased Douglas-fir water stress. The magnitude of this response varied across sites; the dry site had the greatest shifts in Senecio biomass partitioning, the highest observable water depletion, and the greatest amount of Douglas-fir water stress. The presented results can be useful for determining effective forest vegetation management regimes by

considering the impact of Senecio presence on Douglas-fir seedling drought stress across different site conditions.

Keywords: Vegetation Management · Invasive Species · Water Stress · Competition · Reforestation

Declarations

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Introduction

The use of forest vegetation management (FVM) is an important component of reforestation programs in the United States Pacific Northwest (PNW). The PNW has a Mediterranean climate and competition between tree seedlings and vegetation can be intense during the annually occurring prolonged summer drought (Newton and Preest 1988; Dinger and Rose 2010). Competition for soil water resources between newly planted tree seedlings and aggressive early-seral plants can create drought conditions that impact tree seedling physiology, growth, and likelihood of mortality. Dinger and Rose (2010) demonstrated that at least one pre-planting fall site preparation (FSP) or post-planting spring release (SR) herbicide application improved Douglas-fir seedling growth, soil moisture levels, and water potential values compared with the controls. 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 growing season, and 7.7% in the second growing season. Additionally, research has shown that these FVM treatments applied during stand establishment can have long-term impacts on the growth and biomass accumulation of Douglas-fir stands (Newton and Preest 1988; Rose et al. 2006; Maguire et al. 2009; Dinger and Rose 2010; Goracke 2010; Flamenco et al. 2019; Wightman et al. 2019). The magnitude of this response, however, often varies with site conditions such as climate, soil type and vegetation community.

Senecio sylvaticus [L.] (Senecio) is one of the most widespread and aggressive plant colonizers of recently harvested sites in the PNW (West and Chilcote 1968; Dyrness 1973). 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 anthropogenic disturbances such as fire or clearcuting. 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 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 Nelissen 1979).

Many commercially available pre-emergent herbicides do not effectively control Senecio which then rapidly colonizes treated sites where other forms of vegetation have been controlled. For example, in a study conducted by the Vegetation Management Research Cooperative (VMRC) at Oregon State University, plots treated with a FSP herbicide application had 50-60% total vegetation cover the summer after planting, 30-35% of which consisted of Senecio (Wightman et al. 2020). This is a common situation for operational forest lands in the PNW; however, the impacts of Senecio abundance on soil moisture dynamics and planted Douglas-fir seedling performance has not been well documented despite a high potential for growth limitation or seedling mortality.

This study was installed by the VMRC in the spring of 2019 to investigate competition dynamics between newly planted Douglas-fir seedlings and Senecio across a range of site conditions. The specific objectives were: 1) evaluate seasonal dynamics of Senecio cover and height across different environments, 2) develop a function to convert Senecio cover and height to biomass, and 3) determine the interactive effect of Senecio presence and site conditions on seasonal soil moisture dynamics and Douglas-fir drought stress.

Methods

Site Selection

Three sites with varying climates and soils across Western Oregon were selected for the study. The study areas were located in newly planted Douglas-fir plantations that had received a FSP treatment. The specific tank mixtures are listed at the end of each of the corresponding site description paragraphs below. Within each site, a 0.3 ha study area was identified and excluded from any further herbicide application. By excluding these areas from any post-planting herbicide treatments, a large amount of Senecio was expected at each site.

The first site is situated on a plateau near a steep slope overlooking the town of Sweet Home, OR (SH). 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 at 109 km from of the Pacific Ocean. The site has an annual mean temperature and total rainfall of 10.8°C and 1170 mm, respectively, and summer mean temperature and total rainfall of 17.8°C and 90 mm, respectively (Wang et al. 2012). Soils corresponds to Peavine and Kilchis-Harrington series defined as silty clay loam with stony loam (Soil Survey Staff 2019). Measurements from the upper 20 cm of soil at the site estimated the particle size distribution to be 31% sand, 33% silt, and 36% clay. Observations also indicate that the soil has some areas that contained significant gravel and coarse material. The site was planted in January 2019 with bareroot plug+1 Douglas-fir seedlings (50 cm height). The tank mix used in the FSP herbicide application included 4.66 liters of glyphosate, 1.17 liters of imazapyr, 0.3 liters of Oust Extra and 0.58 liters of MSO per ha. This was applied in September 2018.

The second site is located on a steep SE facing slope near Burnt Woods, OR (BW). This study site is located at 44°35'14.2"N 123°40'57.0"W in the Oregon 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 an annual mean temperature and total rainfall of 10.2°C and 2070 mm, respectively, and summer mean temperature and total rainfall of 16.8°C and 84 mm, respectively (Wang et al. 2012). Soils correspond to the Preacher-Bohannon-Slickrock complex defined as a loam weathered from sedimentary rock types, loam from sandstone, and Slickrock gravelly loam (Soil Survey Staff 2019). Measurements from the upper 20 cm of soil at the site estimated the particle size distribution to be 36% sand, 33% silt, and 31% clay. The site was planted in February 2019 with styro 20 containerized Douglas-fir seedlings (30 cm height) and the tank mix used for the FSP herbicide application included 3.51 liters of glyphosate-5.4, 0.58 liters of Imazapyr 4SL, 0.22 liters of Oust Extra, and 0.44 liters of Syl-Tac per ha. This was applied in August 2018.

The third site is located near Veneta, OR (VN). 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 an annual mean temperature and total rainfall of 11.0°C and 1422 mm, respectively, and summer mean temperature and total rainfall of 18.4°C and 54 mm, respectively (Wang et al. 2012). Soils corresponds to Peavine series defined as a silty clay loam (Soil Survey Staff 2019). Measurements from the upper 20 cm of soil at the site estimated the particle size distribution to be 31% sand, 38% silt, and 31% clay. The site was planted in January 2019 with bareroot plug+1 Douglas-fir seedlings (50 cm height) and the tank mix used in FSP included 5.26 liters of glyphosate-5.4, 0.3 liters of Oust XP and 0.07 liters of MSM 60 per ha. This was applied in August 2018.

Soil Moisture and Weather

In order to assess soil moisture dynamics associated with varying abundance levels of Senecio, 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) during the 2019 growing season. At each site, a circular study area of 0.3 ha was identified with uniform terrain 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 1). One TDR probe was installed in each octant at a random azimuth and distance from the central point (Figure 1). By randomly selecting the location of the 8 soil moisture probes, 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 0.3 ha circular plot at each site, a weather station and datalogger (CR300, Campbell Scientific) was installed to measure and collect all soil moisture and weather information; all data was recorded at 30-minute intervals. Weather measurements included solar global radiation (CS301, Apogee Instruments), air temperature and relative humidity (HMP60, Vaisala), and rainfall (TE525MM, Texas Electronics). 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 throughout 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):

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

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.

Additionally, measurements of soil VWC were taken adjacent to 16 Douglas-fir seedlings (15 cm from the stem; two measurements per seedling) at each site on each of the water potential measurement dates described below using a handheld TDR soil moisture sensor (HS2, Campbell Scientific; 20 cm probe length) to correlate soil moisture and seedling water potential. 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).

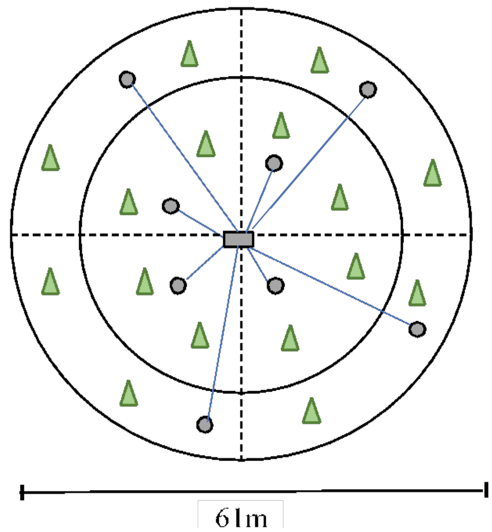

Fig. 1 Diagram of sensors deployment in the study area (0.3 ha) at each site. Soil moisture sensors were deployed in two rings with the same area. The central grey rectangle represents the weather station with a datalogger. Gray circles represent the soil moisture sensors. Green triangles represent the Douglas-fir seedlings where soil moisture and water potential were assessed

Senecio and Douglas-fir Xylem Water Potential

Within the circular plot at each site, 16 Douglas-fir seedlings, that were surrounded by varying amounts of Senecio, were selected for monthly measurements of predawn (Ψ_{PD}) and midday (Ψ_{MD}) xylem water potential between June and September (Figure 1). Additionally, five Senecio plants within the study area were randomly selected on each measurement date for Ψ_{PD} and Ψ_{MD} measurements. Xylem water potential measurements were conducted using a pressure chamber (Model 600, PMS Instrument Co.) and Ψ_{PD} measurements were taken approximately two hours before dawn while Ψ_{MD} measurements were taken during solar noon on each measurement date. For both Ψ_{PD} and Ψ_{MD} measurements, one live branchlet from each seedling was excised with a razor and put into a foil-laminated zip-lock bag and measurements were taken within 2 minutes of branchlet excision.

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:

$$WSI = \sum(\Psi_{i,i+1} - c) \cdot n \qquad (2)$$

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}).

Senecio Cover and Biomass Dynamics

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 frame. Cover was defined as the visual obfuscation of the soil by plant vegetative matter on a 2-dimensional plane; the amount of soil that was covered was noted as a % of the 1x1 m square frame. 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 selected and sampled every two to three weeks during the study period to develop equations to convert Senecio cover percent and height (% m) to biomass (Mg ha^{-1}). Clip plot locations represented the range of Senecio abundance found across the study area at each of the three sites. 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 for 72 hours at 65°C before being weighed. A power model was selected to describe the relationship between Senecio biomass and cover %:

$$\mathrm{SB} = a \cdot (\mathrm{CxH})^{b} \qquad (3)$$

where SB is the aboveground biomass (Mg ha^{-1}), C is the cover (%), H is height (cm) of Senecio, and a and b are regression parameters. This model was selected after testing several linear and non-linear equations.

To quantify individual plant allometry, during September 2019, 10 complete Senecio and Douglas-fir individuals at each site were excavated and taken back to the laboratory for morphology and biomass measurements. Photos were taken of each fresh sample's root system and used to measure the number of root tips using WinRHIZO image analysis system (WinRHIZO Pro, Regent Instruments). Measurements were taken of the total stem height (H, cm), the number of root tips larger than 1 mm (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 also measured using the water displacement method (Harrington et al., 1994). After these initial measurements, all plants were oven-dried at 65ºC for 72 hours and weighed to get aboveground (AGB, g) and belowground (BGB, g) dry mass. 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:

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

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

Soil Water Depletion 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 depletion by 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 day. Senecio data (cover % and height measured every two to three weeks) was estimated for each day at each sampling point using linear interpolation between measurement dates and was then merged with soil water and climate data.

Statistical Analysis

Model development and statistical tests were performed using SAS version 9.4 (PROC GLM and PROC NLIN). Several models (linear and non-linear) were tested to correlate Senecio cover x height with other response variables: Linear models were used to correlate Senecio cover x height with cumulative soil water depletion and Douglas-fir Ψ_{PD}. Non-linear model fitting was used to estimate Senecio biomass from cover x height. Linear regression was also used to calibrate handheld TDR VWC readings with values from the soil cores. Two-Way Analysis of Variance (ANOVA) with Tukey Post-Hoc tests were used to determine the effect of species, site, and the interaction of species by site on Douglas-fir and Senecio Ψ_{PD}, Ψ_{MD}, morphology, and biomass. Repeated measures analysis was used to analyze time series data. Several covariance structures were tested for the time series analysis and the variance component structure was selected as it showed the lowest Bayesian information criterion (Littell et al. 1996). All significance tests used $\alpha = 0.05$. Sigmaplot version 14 (Systat Software, Inc.) was used to make all figures.

Results

Weather Conditions

Weather variables differenced among the sites from April to late September (weekly mean values are shown in Figure 2). The VN site had the highest VPD and temperature and lowest relative humidity and rainfall, with little-to-no rain from the first of June until the beginning of September. The SH and BW sites had more precipitation events than the VN site, especially in June which recharged soil moisture 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 (Figure 2d). The mean RH was 72, 75 and 81% for the VN, SH and BW sites, respectively (Figure 2b). The mean growing season temperature for VN, SH and BW sites was 16.8, 16.1, and 16.2 ºC, respectively (Figure 2c).

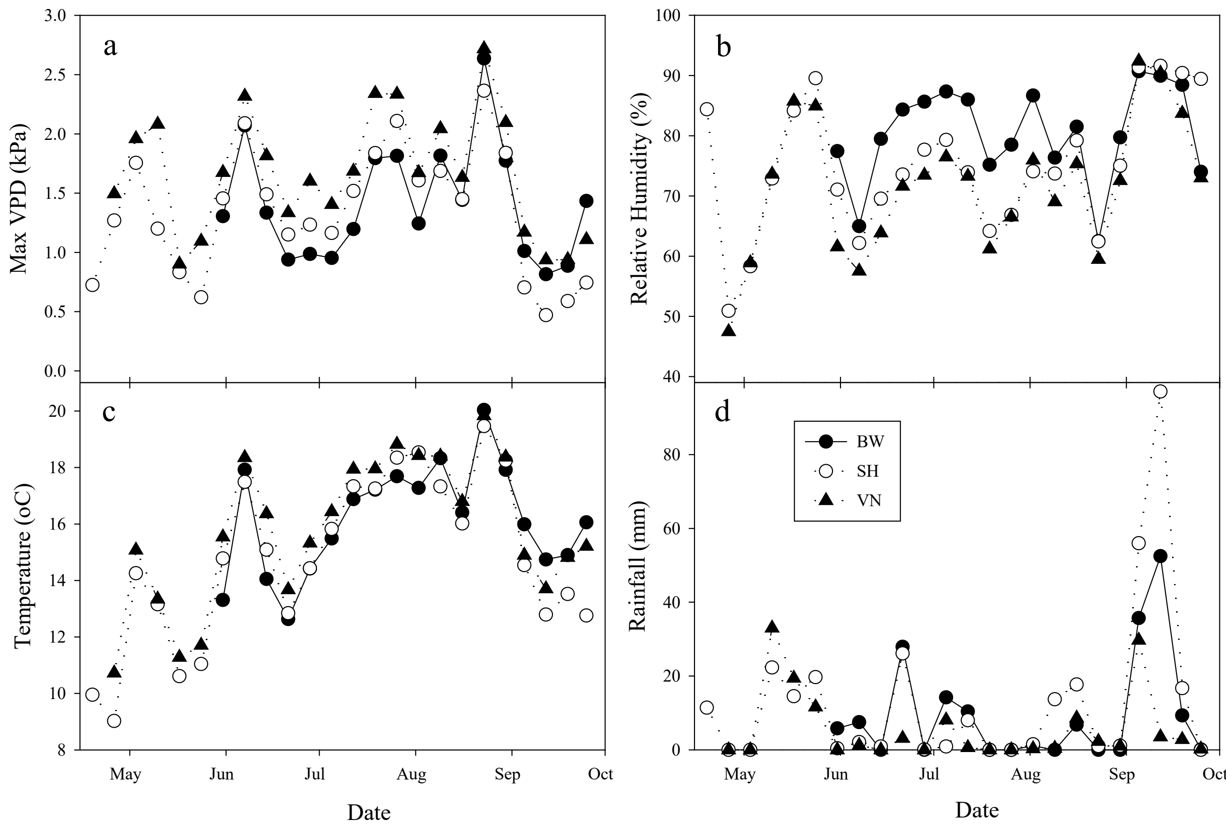

Fig. 2 Weekly: a) mean maximum daily VPD, b) mean daily relative humidity, c) mean daily air temperature and d) total rainfall, for the BW (filled circle), SH (open circle) and VN (filled triangle) sites

Seasonal Dynamics of Senecio Cover and Height

Within a 1 m^2 area, trees had lower average amounts of Senecio than soil moisture probes (data not shown). This is likely due to the presence of the planted Douglas-fir seedlings. Therefore, because of the Douglas-fir seedling presence influencing Senecio dynamics, results for seasonal vegetation dynamics are only presented for the probe centered surveys. At the start of the study, there was little-to-no Senecio at the sites. Senecio florets were only a few centimeters wide and tall by late April; however, as the growing season progressed, these florets grew rapidly achieving heights of over 100 cm in July at the BW site (Figure 3).

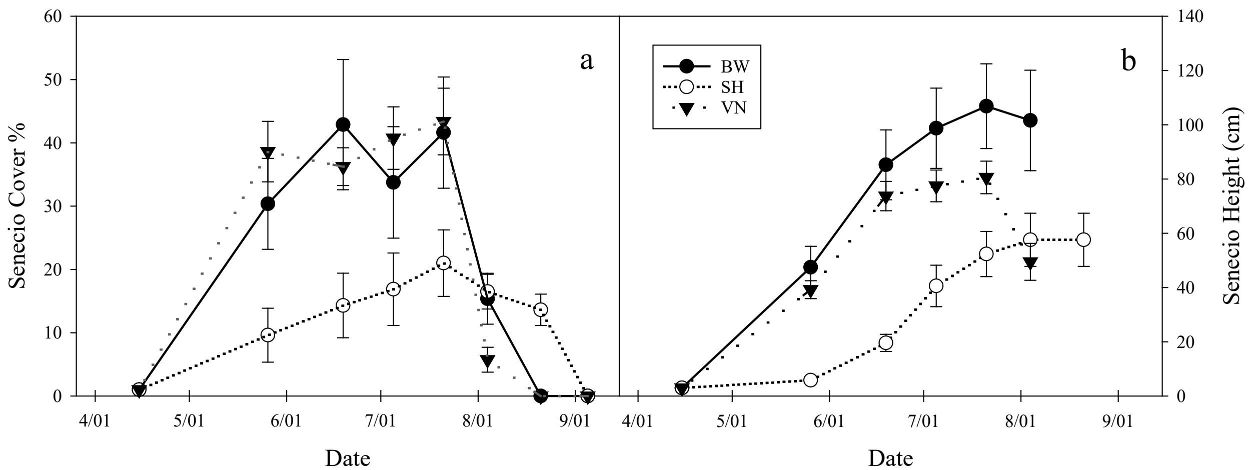

Fig. 3 Seasonal dynamics of: a) cover (%) and b) height (cm) for Senecio growing at the BW (filled circle), SH (open circle) and VN (filled triangle) sites. Error bars represent standard error. Measurements were centered on soil moisture probes (n=8)

There was a significant site by measurement date interaction for Senecio cover (P=0.003) indicating that the growth dynamics of Senecio during the 2019 growing season were different across the sites (Figure 3a). Senecio cover at BW and VN did not differ at any date (P>0.216) and increased rapidly reaching maximum values of 43% cover in mid-June. This cover was maintained until mid-July after which senescence decreased the average cover to 15.4% at BW and 5.8% at VN by early August. The development of Senecio cover at the SH site was slower than the other sites with values of cover steadily increasing and not reaching the maximum average of 21% cover until mid-July (Figure 3a). Senecio cover was lower at SH than the other sites from late-May to mid-July (P=0.031); however, senescence also began to occur at SH after Mid-July resulting in no significant difference among the sites in Senecio cover in August (P=0.167). There was a marginally significant site by measurement date interaction for Senecio height (P=0.056) indicating differences in height development among the sites (Figure 3b). Senecio height at BW and VN increased over time until mid-July after which height decreased due to senescence. At SH Senecio height increased over time and did not reach maximum values until August. Senecio height did not decrease at SH, showing no evidence of senescence. Maximum height of Senecio differed among the sites (P=0.007), averaging 107, 58 and 81 cm, for BW, SH and VN sites, respectively.

Senecio Aboveground Biomass per Unit Ground Area

There was a strong relationship (P<0.001, R^2=0.93) between Cover x Height (CxH, % m) and aboveground biomass (AGB_{-SESY}, Mg ha^{-1}) of Senecio, which was shared across sites using the following function: $AGB_{-SESY} = 0.0495 \cdot (CxH)^{1.110}$ (Figure 4a). Using the function presented in Figure 4a and data presented in Figure 3 we were able to calculate the seasonal dynamics of Senecio aboveground biomass at the sites (Figure 4b). Senecio aboveground biomass dynamics followed a similar trend to that of Senecio cover.

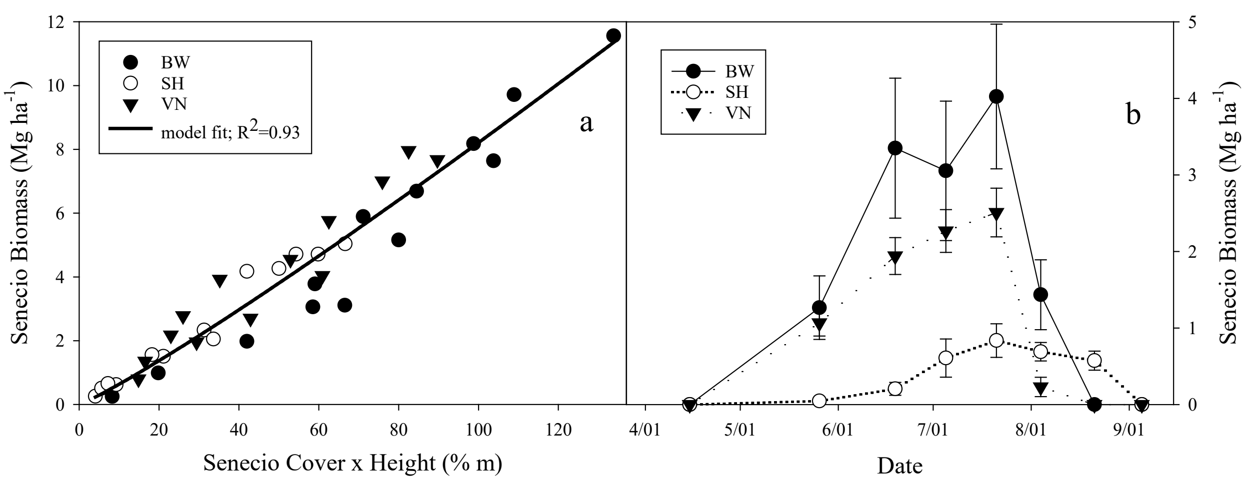

Fig. 4 a) relationship between cover x height (% m) and aboveground biomass (Mg ha^{-1}) and b) seasonal dynamics of aboveground biomass (Mg ha^{-1}) for Senecio growing at the BW (filled circle), SH (open circle) and VN (filled triangle) sites. Error bars represent standard error.

Senecio and Douglas-fir Biomass and Root Architecture

Table 1 provides 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 and shoot:root ratio (P=0.002 and 0.031, respectively), implying that the species responded differently to the site conditions for these variables. There were also differences between sites within species; for example, Douglas-fir seedlings growing at the SH site had two times more BGB than those growing at the BW site (P<0.001), likely due to differences in stock type. BGB of Senecio plants was not different across sites (P=0.370). Senecio shoot:root ratio was the highest at BW and this difference was significant when compared to VN (P=0.009), and nearly so when compared to SH (P=0.087). However, for Douglas-fir, the shoot:root ratio did not significantly differ across sites. There were also significant differences in Ntips (>1 mm) between species (P=0.020).

Senecio had significantly higher root volume than Douglas-fir (P=0.004); Senecio had an average of 30.3 cm^3, while Douglas-fir had an average of 15.2 cm^3. However, Douglas-fir had a much higher average root biomass of 21.5 g, while Senecio average root biomass was 5.9 g (Table 1). It is worth noting that although Douglas-fir had more BGB, the RHL was significantly lower than that of Senecio (P<0.001; Table 1). The average RHL of Douglas-fir was 14.6 cm and Senecio average RHL was 29.3 cm (P<0.001, Table 1). On the other hand, RVL was not significantly different across species or sites (P=0.780, Table 1) averaging 25.1 and 24.5 cm for Douglas-fir and Senecio, respectively.

Table 1 Mean values ± standard error of aboveground biomass (AGB, g), belowground biomass (BGB, g), shoot to root ratio (shoot:root, g g^{-1}), number of root tips larger than 1 mm (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 Western Oregon. Summary of ANOVA P-values for the main effects of site, species, and their interaction is also provided for each variable.

Species	Site	AGB g	BGB g	shoot:root g g^{-1}	NTips	RV cm^3	RHL cm	RVL cm	AI cm^2
Douglas-fir	BW	19.9 ± 2.2	14.9 ± 2.2	1.5 ± 0.2	28.2 ± 2.1	16.1 ± 2.6	11.9 ± 1.6	29.2 ± 1.4	241.7 ±
	SH	46.9 ± 5.5	31 ± 3.0	1.6 ± 0.1	40.5 ± 4.2	16.2 ± 3.3	19.4 ± 2.1	24.2 ± 1.8	512.2 ±
	VN	27.9 ± 3.1	18.5 ± 2.0	1.5 ± 0.1	30.1 ± 3.4	13.4 ± 2.8	12.6 ± 1.7	21.8 ± 1.4	268.7 ±
Senecio	BW	52.6 ± 14.3	4.1 ± 1.1	12.4 ± 1.4	13.1 ± 2.0	25.3 ± 6.4	29.4 ± 4.9	24.15 ± 3.4	620.8 ±
	SH	51.3 ± 12.0	6.0 ± 1.7	10.6 ± 1.4	9.9 ± 1.8	30.5 ± 6.4	28 ± 4.6	21.7 ± 2.4	774.9 ±
	VN	53.6 ± 10.8	7.5 ± 1.5	7.7 ± 0.9	10.1 ± 2.1	35.0 ± 6.1	30.6 ± 3.7	27.7 ± 3.4	639.9 ±
ANOVA P>F*	Factor								
	Site	0.371	<0.001	0.030	0.716	0.760	0.653	0.320	0.97
	Species	**0.008**	<0.001	<0.001	**0.004**	**<0.001**	**<0.001**	0.784	**<0.00**
	Site*Species	0.285	**0.002**	**0.031**	0.066	0.449	0.299	0.073	0.75

Overall, Senecio across all sites had approximately 2 times the root area of influence per individual plant compared to Douglas-fir (P<0.001, Table 1). The average area of influence for Douglas-fir roots was 341 cm^2, which makes it 2 times smaller than Senecio's average root area of influence of 679 cm^2.

Soil Water Dynamics

There was a consistent pattern across the sites where FASW values were reduced as the magnitude of Senecio abundance increased (Figure 5). At each site during the beginning of the growing season, maximum values of FASW (when VWC is equal to DUL) were achieved, but values of FASW quickly separated as the dry season progressed with probes surrounded by higher levels of Senecio having faster reduction in FASW (Figure 5). This effect was most pronounced at the dry site (VN) which indicates the interactive effect of Senecio and environmental conditions on FASW.

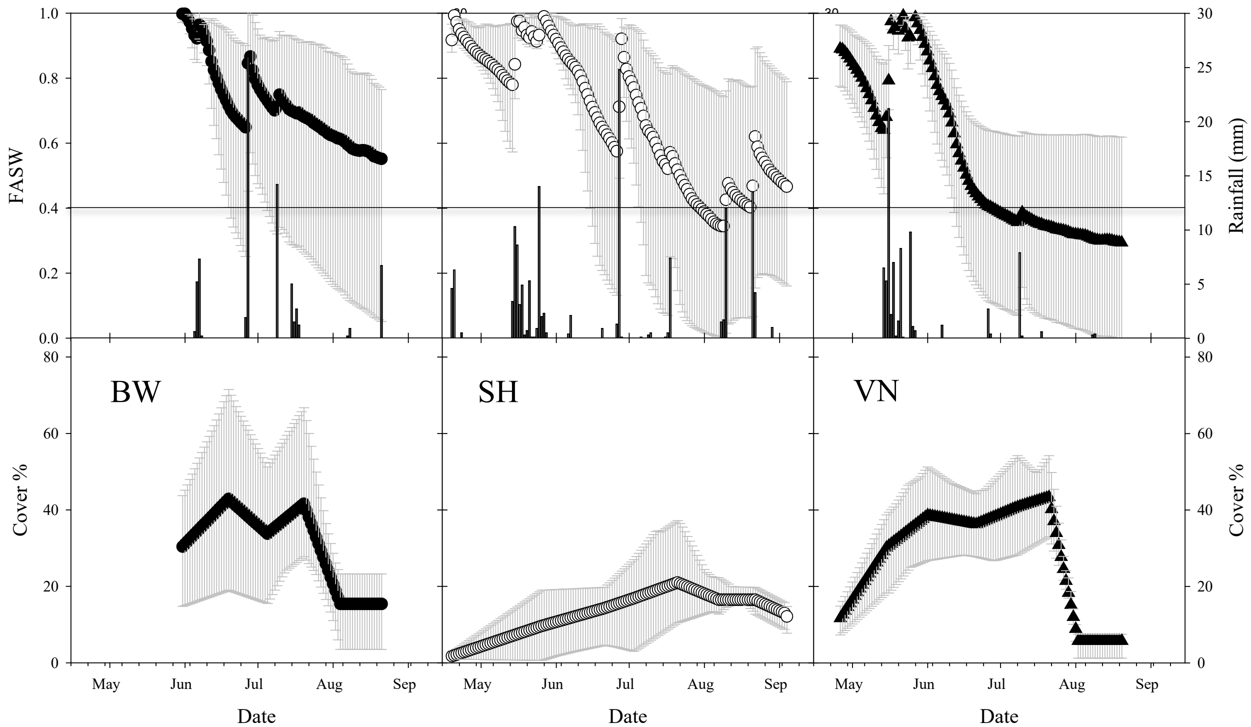

Fig. 5 Seasonal dynamics of soil moisture (expressed as fractional available soil water of 0-30 cm soil depth, FASW; upper panel) and Senecio abundance (expressed as cover %; lower panel) at the BW (left, filled circle), SH (center, open circle) and VN (right, filled triangle) sites. Error bars represent the range of maximum and minimum observed values. On the top panels, bars depict daily rainfall (mm)

Independent of site, at some point during the growing season FASW was reduced to 0 in areas with high abundance of Senecio (Figure 5). Furthermore, each site had probes that were at or lower than 0.4 FASW during the summer from July until the end of the measurement period. The driest site (VN), was consistently below 0.4 FASW from July 1st until the end of the measurement period (Figure 5). The probe with the highest % Senecio cover at VN was below 20% FASW from 6/14 to the end of the growing season. This extended the drought period by about a month compared to the other sites, both of which did not drop below 20% FASW in areas of high Senecio cover until the middle of July (SH: 7/7; BW: 7/10). Rainfall events also recharged FASW multiple times over the drought period at the BW and SH sites (Figures 2 and 5) and is the main reason the soil moisture at these sites did not reach low values of FASW for as long as the

VN site did.

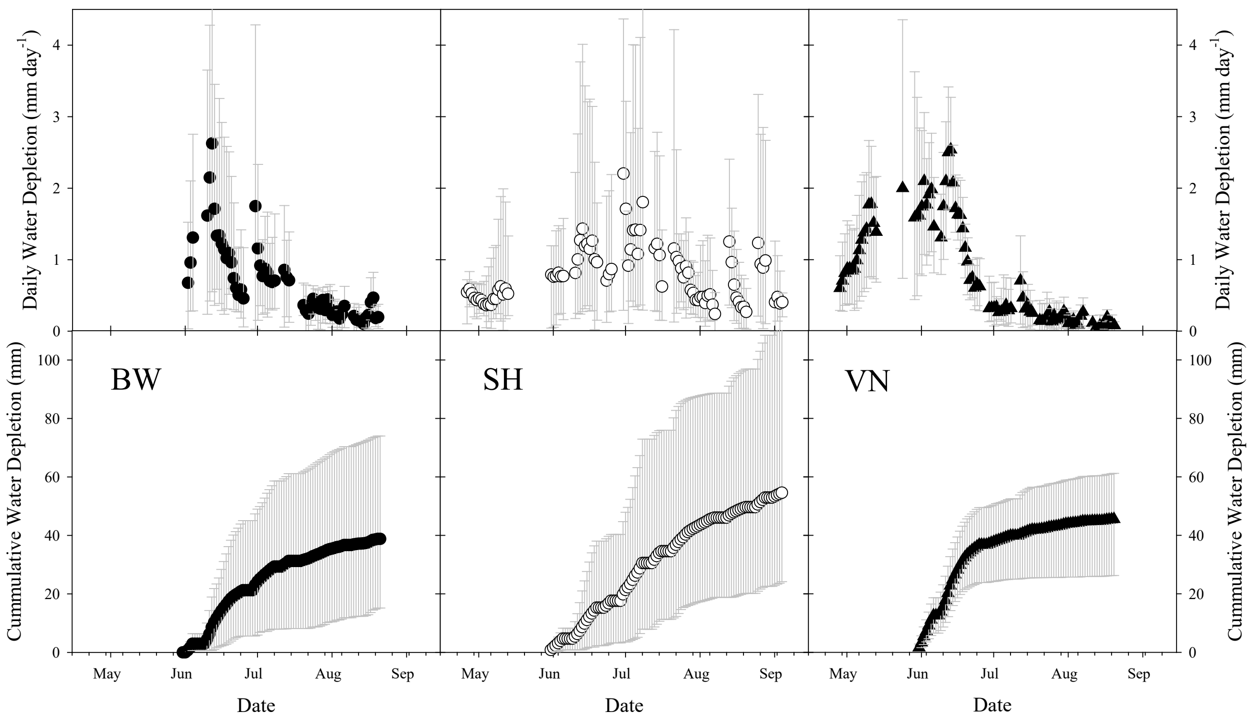

Fig. 6 Seasonal dynamics of daily water depletion (mm day^{-1}) and cumulative water depletion (mm) of the top 30 cm of soil at the BW (left, filled circle), SH (center, open circle) and VN (right, filled triangle) sites. Error bars represent the range of maximum and minimum observed values

Figure 6 illustrates the different amounts of cumulative water depletion of the top 30 cm of soil at each site as a result of Senecio's presence. There was an interactive effect of time (day of the year) and site on cumulative water depletion ($P<0.001$), meaning that the water use of Senecio was different across sites at different dates during the growing season. This analysis was conducted with data between 6/1 and 8/22 as all Senecio had senesced at the VN and BW sites by 8/22. At SH, there was still a large living Senecio population into September.

Cumulative water depletion was greater at VN than at SH from 6/14 through 7/3 ($P<0.042$) and VN was greater than BW from 6/17 through 6/30. There were no other significant differences among the sites in cumulative soil water depletion between 6/1 and 8/22, but Senecio at SH survived later into the growing season and continued to deplete soil water through the last measurement on 09/04. This resulted in a steadier and prolonged reduction in soil water at SH than the other sites. In contrast, the effect of Senecio senescence in July at VN and BW sites resulted in a reduction in the rate of soil water depletion during July which persisted through August (Figure 6). Across all soil moisture measurement points, the average total soil water depletion was 46, 55 and 38 mm at the VN, SH and BW sites, respectively. The number of days of effective data recorded was 64, 60 and 46 days, giving an average water depletion of 0.7, 0.9 and 1.3 mm day^{-1} on days without rainfall at the VN, SH and BW sites, respectively. During the period of peak Senecio abundance (6/3-6/22) soil water depletion rates were higher averaging 1.6, 1.0 and 1.3 mm day^{-1} for the VN, SH and BW sites, respectively. At this time, the average Senecio cover was 37, 13 and 36% at the VN, SH and BW sites, respectively.

Figure 7 shows the relationship between peak Senecio abundance in July and cumulative soil water depletion between 6/1 and 8/30. In general, higher soil water depletion was observed in areas with higher Senecio abundance. This relationship differed across sites ($P<0.001$) such that the effect of Senecio cover on soil water depletion was much more dramatic at SH than at BW and VN which did not differ.

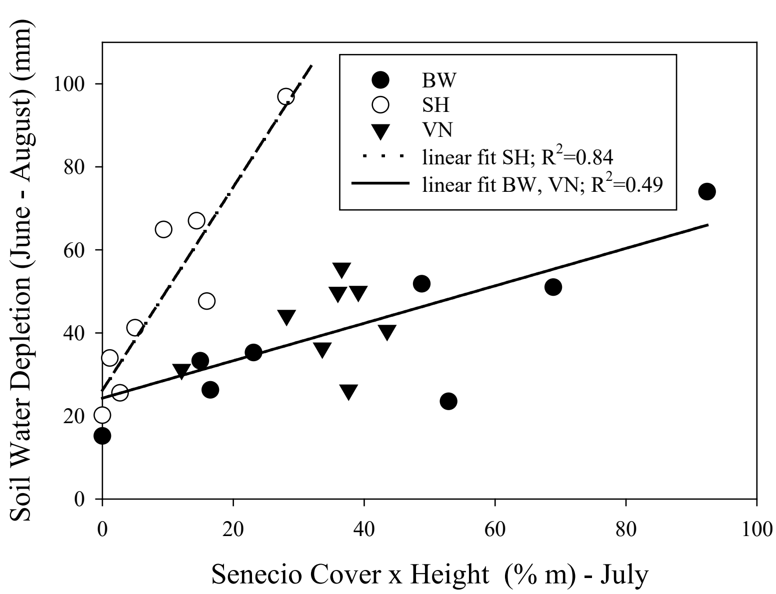

Fig. 7 Relationship between Senecio cover by height (% m, measured in July), and cumulative soil water depletion (mm, from June 1 to August 30), at the BW (filled circle), SH (open circle) and VN (filled triangle) sites

Senecio and Douglas-fir Xylem Water Potential

Seasonal variation in xylem water potential is shown in Figure 8 (from 06/01 to 09/05). 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 water status was different between Douglas-fir and Senecio for the different sites at different dates during the growing season. For example, at the BW and SH 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 lower Ψ_{PD} than Senecio (P<0.001 and P=0.009, respectively). 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 (P<0.001).

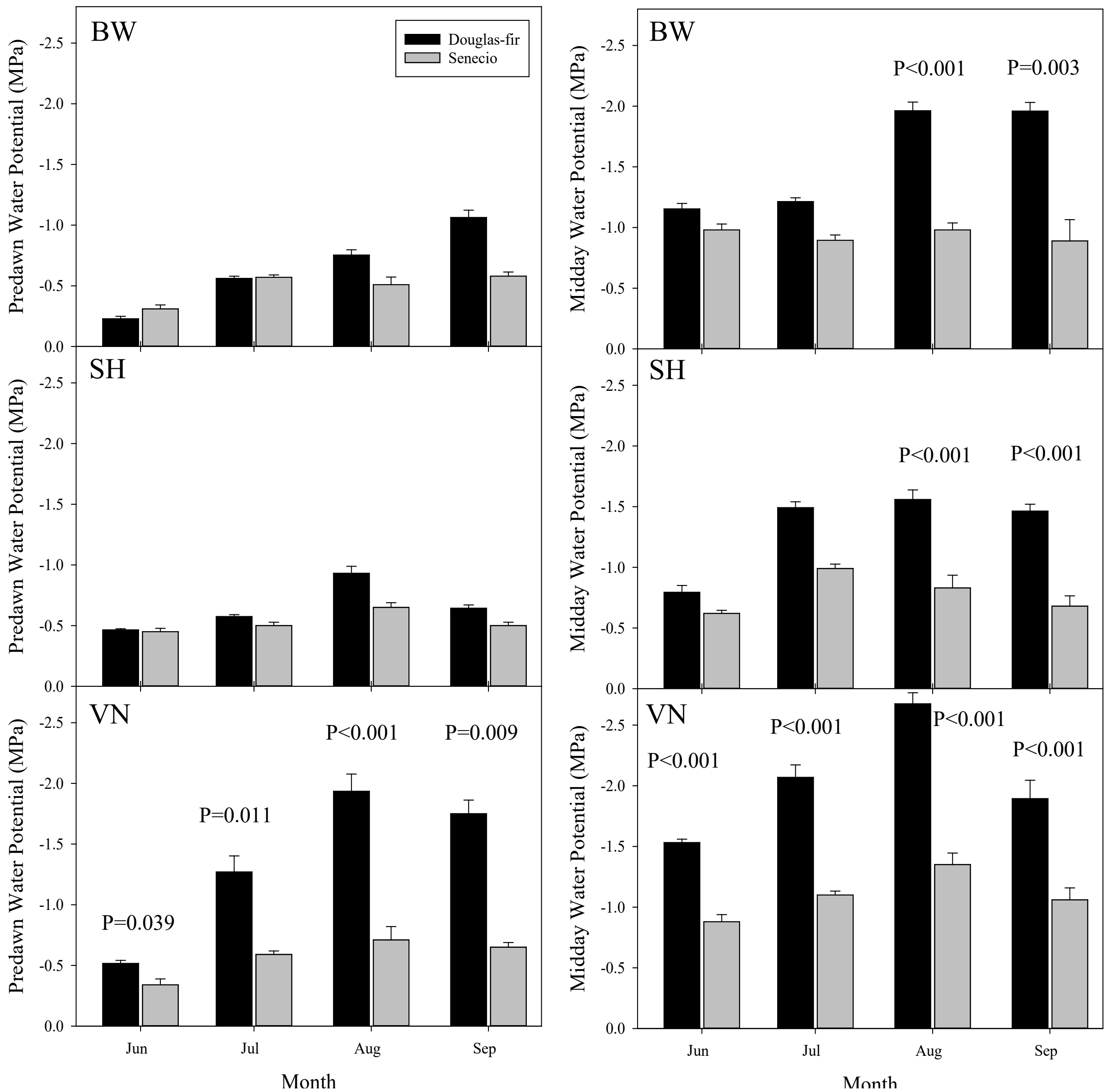

Fig. 8 Predawn (left) and midday (right) xylem water potential of Douglas-fir (black bar) and Senecio (grey bar) growing at the BW (upper panel), SH (middle panel) and VN (lower panel) sites. Error bars represent standard error. P-values for significant differences between species are shown on top of each pair of columns

There was a strong relationship between Senecio abundance and Douglas-fir water stress, and that relationship was different across sites (Figure 9). For the VN site for every increase of 10 CxH (% m) of Senecio, Douglas-fir Ψ_{PD} decreased by 0.5 MPa ($P<0.001$; $R^2 = 0.66$; Figure 9). At the SH site, for every increase of 10 CxH (% m) of Senecio, Douglas-fir Ψ_{PD} decreased by 0.35

MPa ($P<0.001$; $R^2 = 0.88$; Figure 9). On the other hand, at the BW site, the relationship was weak, showing for every increase of 10 CxH (% m) of Senecio, Douglas-fir Ψ_{PD} decreased by 0.05 MPa ($P=0.017$; $R^2 = 0.34$; Figure 9). In sites such as VN, which experienced limited rainfall during the growing season, having 30% cover of 1 m tall Senecio will result in the Douglas-fir seedlings having Ψ_{PD} of -2.4 MPa.

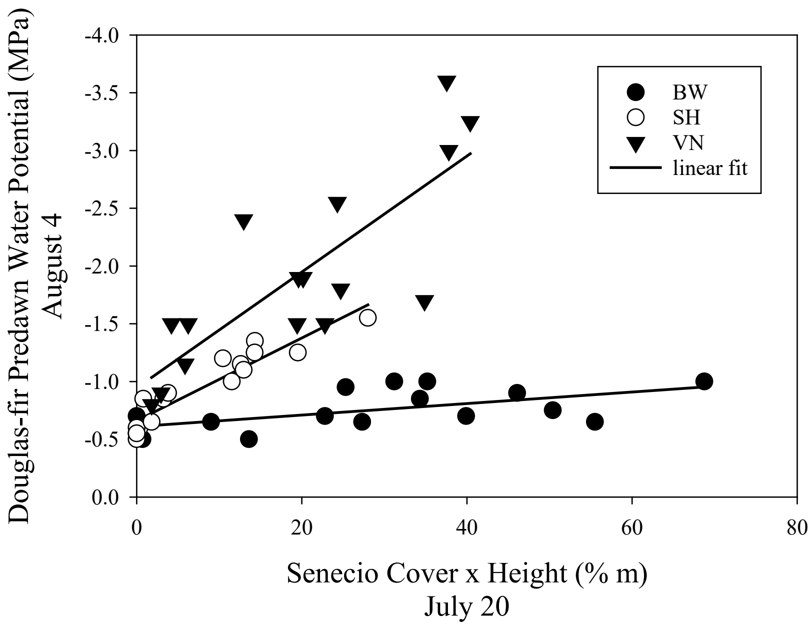

Fig. 9 Relationship between Cover x Height (% m) of Senecio in July and Predawn Water Potential (MPa) of Douglas-fir seedlings in August at BW (filled circle), SH (open circle) and VN (filled triangle) sites

There was a significant interaction between species and site for WSI_{PD} at the end of the evaluation period ($P<0.001$). Douglas-fir seedlings growing at the VN site had a WSI_{PD} 2.4 times larger than seedlings growing at the BW and SH sites (140 vs. 57 and 58 MPa day, respectively), while Senecio WSI_{PD} was not affected by site. There was, however, a strong relationship between WSI_{MD} measured at the end of the growing season and the shoot:root ratio and root mass of Senecio across the three study sites (Figure 10). These results indicate that as the cumulative seasonal water stress (WSI_{MD}) increased, Senecio shoot:root ratio decreased and root mass increased. This response was not seen for Douglas-fir which had similar shoot:root across sites: 1.62 for SH, 1.51 for VN, and 1.51 for BW (Table 1).

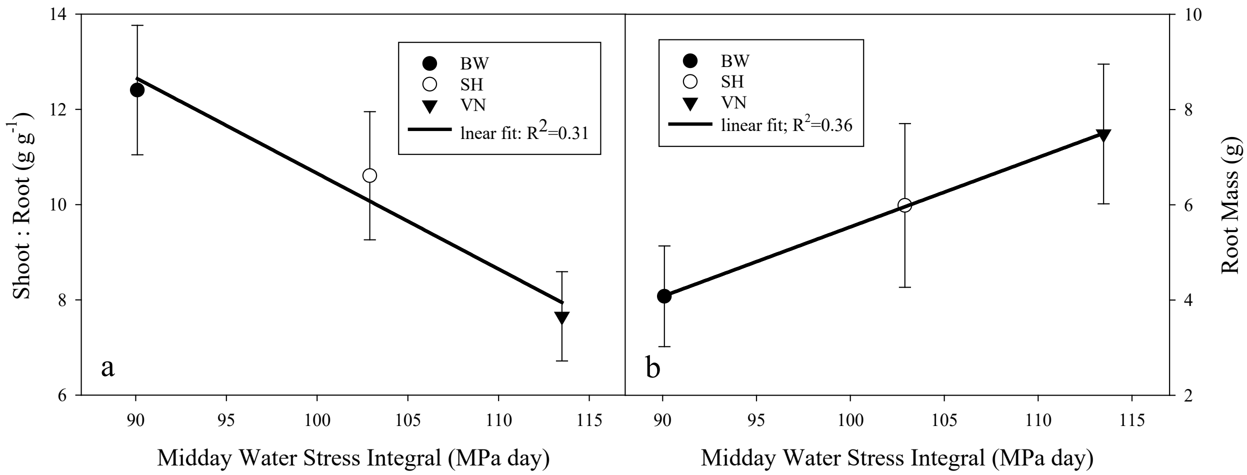

Fig. 10 Relationship between midday water stress integral (WSI_{MD}, MPa day) a) and shoot to root ratio (g g^{-1}) and b) root mass (g) at the end of the growing season for Senecio plants growing at the BW (filled circle), SH (open circle) and VN (filled triangle) sites

Discussion

This study demonstrated that growth and competition dynamics of Senecio varies across sites in the United States PNW and that Senecio presence can reduce soil water availability and increase water stress of newly planted Douglas-fir seedlings. The weather conditions at the three sites varied such that the summer drought was more intense at the VN site than the BW and SH sites as reflected in lower rainfall and higher VPD (Figure 2). The SH site had higher rainfall than the other sites, especially during August. These differences in weather produced differences in Senecio growth dynamics with BW and VN having a seasonal pattern of Senecio abundance that can be described as undergoing rapid early growth plateauing early in the summer followed by rapid senescence in late July (Figure 3). In contrast, growth dynamics at the SH site showed a slower Senecio colonization rate with values of cover and height gradually increasing throughout the growing season followed by the germination of a second cohort of Senecio in August. This plasticity of Senecio allows it to grow well on sites with varying climates and soils and is one of the features that makes it such a strong competitor throughout the region (West and Chilcote 1968; Hanson 1998).

The Senecio biomass function developed in this paper used the simple inputs of cover and height to predict Senecio aboveground biomass. Interestingly, this function was shared across all three sites despite differences in the seasonal dynamics and abundance of Senecio. Using this function we calculated seasonal biomass dynamics with peak values in mid-July averaging 3.8, 1.0 and 2.9 Mg ha^{-1} for the BW, SH, and VN sites, respectively. A different study conducted by the VMRC reported that forb biomass averaged 1.1 and 1.4 Mg ha^{-1} in areas without herbicide application during the first two years following timber harvest at two sites in Western Oregon (Guevara et al. 2021). When other growth habits were included, they reported total vegetation biomass averaged 4.3 and 5.2 Mg ha^{-1}. Considering that our study sites received a FSP herbicide application, the levels of biomass at the BW and VN sites are high. This reflects Senecio's ability to rapidly occupy a site, often growing at a density of 22 individuals per m^2 (Dinger 2012).

The seasonal pattern of Senecio water use, reflected in soil water depletion, differed among sites due to differences in weather and Senecio growth dynamics (Figures 2, 3, 5 and 6). The rate of soil water depletion at the VN site early in the growing season was much higher than the SH or BW sites even though the BW site had similar Senecio cover. This difference can be explained by the higher evaporative demand at the VN site which had an average VPD that was 29% higher than BW during June (Figure 2). The VN site also only had 4.3 mm of rainfall during June compared to 41.2 mm at BW. Soil water depletion leveled off at the VN and BW sites around mid-July as Senecio senesced. This seasonal pattern of soil water depletion was contrasted by the SH site which showed similar rates of water depletion as the BW site early in the growing season but did not demonstrate the same leveling off during mid-summer. This is likely due to weather conditions at SH allowing for a longer Senecio lifespan and second flush of Senecio during late summer.

There was a strong relationship between the amount of Senecio and the reduction in soil moisture (Figures 5 and 7). This result is not surprising as the water use of vegetation has been demonstrated to be directly correlated to vegetation cover, and, therefore, leaf area (Hoff et al. 2003; Netzer et al. 2009; Palmer et al. 2010; Thrippleton et al. 2018). Figure 7 illustrates this point, but the slope of the relationship differed among sites with SH having a steeper slope than BW and VN. This difference in the relationship between Senecio cover and water use is likely due to the longer lifespan and second flush of Senecio at the SH increasing cumulative soil water depletion (Figure 6).

Average Senecio water use during the peak of Senecio abundance (6/3 to 6/22) ranged from 1.0 mm day^{-1} at BW to 1.63 mm day^{-1} at VN. This rate of water use is within the range of average transpiration rate of invasive annual and native perennial species in California, with values of 0.84 mm day^{-1} and 0.81 mm day^{-1}, respectively (Everard et al. 2010). Everard et al. (2010) found that the maximum transpiration rate was 2.6 mm day^{-1} for invasive annuals and 0.81 mm day^{-1} for native perennials. Our maximum daily transpiration rate for Senecio was seen at BW with a value of 2.67 mm day^{-1} (Figure 5). These results demonstrate that Senecio is highly competitive for soil water with transpiration rates near the maximum values reported for other herbaceous species.

The impact of Senecio water use on the drought stress of Douglas-fir seedlings varied across sites and time. For instance, Douglas-fir seedlings at VN had a WSI_{pd} approximately 2.4 times higher than the other sites. Douglas-fir Ψ_{MD} was also below -2.0 MPa for much of the growing season at VN which can have negative consequences on seedling performance and growth as Douglas-fir has been shown to start closing stomata at -1.0 MPa and completely close stomata at -2.0 MPa (Lassoie 1982). Domec et al. (2004) reported that below a threshold Ψ_{MD} of -1.7 MPa, a sharp increase in root embolism was associated with stomatal closing for Douglas-fir trees and that Douglas-fir roots can lose over 60% of maximum hydraulic conductance at a xylem water potential of -2.0 MPa. Shainsky and Radosevich (1992), reported that stem growth of Douglas-fir seedlings stopped at a Ψ_{PD} of -1.6 MPa. The Ψ_{PD} of Douglas-fir at the VN site averaged -1.3 MPa at the start of July and -1.9 MPa at the start of August. These results demonstrate that the rapid depletion of soil water by Senecio at the VN site produced intense drought stress on the Douglas-fir seedlings. The impact of Senecio on Douglas-fir drought stress was less pronounced at the BW and SH sites where seedling Ψ_{PD} averaged near or below -1.0 MPa throughout the entire growing season. This is likely due to the higher rainfall and lower evaporative demand at these sites increasing soil water availability. For example, FASW never averaged less than 0.55 at BW while this value was reached at the VN site by mid-June and continued to drop to 0.39 by the end of June (Figure 5). The BW site was the most costal site, had the highest RH, and experienced frequent fog events which may help explain the contrasting FASW dynamics at BW and VN despite having similar amounts of Senecio.

The seasonal pattern of Ψ_{PD} and Ψ_{MD} differed between Senecio and Douglas-fir reflecting their different life histories. While Douglas-fir water potential tended to decrease throughout the growing season, Senecio Ψ_{PD} and Ψ_{MD} remained relatively stable (Figure 8). This was particularly apparent at the dry VN site where Senecio Ψ_{PD} and Ψ_{MD} were stable, and less than that of Douglas-fir on all measurement dates. This difference between species is almost certainly due to differences in root architecture. The Douglas-fir seedlings in this study were grown in a nursery (containerized and bareroot) and planted at the sites the winter prior to study installation and therefore began with dense roots inserted into the planting hole. In contrast to this, Senecio developed from seed and produced root systems with a distinct pattern of horizontal development, increasing the exploitive efficiency of the root system. As Turner and Kramer (1980) noted, 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 by having an average area of influence 2 times larger than that of Douglas-fir despite there being no differences between the species in mean root vertical length (Table 1). Our study areas represent operational plantations and although the BW site was planted with smaller containerized seedlings compared to the larger bareroot seedlings at the other sites, we believe this difference in seedling morphology did not have a significant effect on seedling physiology although further research is needed in this area.

Senecio not only produced more far-reaching root systems but was also more responsive to environmental conditions. The reported relationship between Senecio WSI_{md} and shoot:root demonstrates that Senecio allocated proportionally more resources to root development as drought stress increased, while Douglas-fir shoot:root was unaffected by WSI_{md} (Figure 10). Changes in plant biomass allocation in response to drought has been reported by others (Newton and Preest 1988; Chan et al. 2003). For instance, Eziz et al. (2017) conducted a meta-analysis on plant biomass allocation with data from 164 published papers and reported an average increase in root mass fraction of 9% in response to drought. In this study, Senecio root mass fraction increased by 5% from the wettest (SH, 7%) to the driest (VN, 12%) sites. The contrasting plasticity of the species may also be related to their life histories: Senecio being an aggressive annual species that rapidly captures resources and produces seed before senescing while Douglas-fir is a long-lived slower growing species that preferentially allocates resources in a different manner. The combination of a more expansive root system, higher plasticity, and annual life history resulted in

Senecio having a Ψ_{PD} that was almost a third of that of Douglas-fir at the VN site during August despite growing under the same weather conditions.

This study demonstrated that a given abundance of Senecio does not always have the same impact on Douglas-fir. The high biomass values at BW, for instance, did not correspond to the highest levels of Douglas-fir drought stress. The results from this study can help inform management decisions on a site-specific context when determining the appropriate amount of control and tolerated abundance of competing vegetation. Senecio's depletion of soil water and inducement of Douglas-fir drought stress can likely 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 and have conditions similar to those at the VN site. For example, Dinger and Rose (2009) found that a single post planting herbicide application significantly increased seedling growth. These type of release treatments limit or even eliminate the impact of Senecio on early Douglas-fir growth allowing the seedlings to better capture site resources which can produce long-term effects on stand development (Flamenco et al. 2019; Wightman et al. 2019).

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