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Comparative effects of soil resource availability on physiology and growth of Scotch broom (*Cytisus scoparius*) and Douglas-fir (*Pseudotsuga menziesii*) seedlings

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ABSTRACT

Scotch broom (*Cytisus scoparius* (L.) Link) is an invasive, N-fixing shrub in recently harvested Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) forests in the Pacific Northwest. The ability of Scotch broom to dominate a site and displace Douglas-fir in this region may be mediated by site quality and site resource supply. Individual seedlings of Scotch broom (n = 46) and Douglas-fir (n = 46) were planted in a controlled nursery setting and monitored over two years to test the effects of irrigation and fertilization treatments on the physiology and growth of these oft-conflicting species. Overall, Scotch broom remained largely unaffected by resource availability relative to Douglas-fir, which was more sensitive to water and nutrient availability. Scotch broom consistently showed greater assimilation and transpiration rates and plant water potentials than Douglas-fir under all treatments – indicating an elevated ability to acquire soil water resources. The conservative ecology of Douglas-fir resulted in greater water-use efficiency than Scotch broom throughout the experiment, however. Similarly, Douglas-fir crown and height growth started later in the growing season and ended earlier than that of Scotch broom, indicating a longer growing season for Scotch broom but also the importance of resource availability early in the growing season for Douglas-fir given its determinate growth. While Douglas-fir growth reflected the additive effects of increased resource availability, it did not surpass the growth of Scotch broom, which maintained steady growth and biomass accrual under all treatment conditions. The height of Douglas-fir growing under optimized conditions was approximately 40 cm less than that of Scotch broom regardless of treatment regime by the end of the two-year study. This demonstrates how critical early intervention is for land managers in order to control this invasive to avoid Scotch broom overtopping Douglas-fir seedlings during stand establishment.

1. Introduction

Scotch broom (*Cytisus scoparius* (L.) Link) is a ubiquitous invader of early-successional coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) forests of the Pacific Northwest (PNW). A prolific producer of seed with a decades-long viability and rapid early growth, Scotch broom is capable of out-competing native species (Fogarty and Facelli, 1999) and dominating sites (Bossard and Rejmanek, 1994; Richardson et al., 2002; Haubensak and Parker, 2004; Slesak et al., 2016).

Native to the Mediterranean (Tutin et al., 1968), Scotch broom's climate of origin is similar to that of the western PNW. Less than 10% of the total annual precipitation occurs during the summer months in the western PNW (Waring and Franklin, 1979), often making soil water the most important limiting resource during the growing season (Brubaker, 1980). Scotch broom is a generalist, possessing contrasting traits that enable it to both acquire limited soil water resources more effectively and reduce its demand for soil water during periods of scarcity – a plasticity that likely facilitates its global distribution across six continents (Potter et al., 2009). With a rapid biomass accrual (Fogarty and Facelli, 1999), a deep rooting habit (Allen and Allen, 1981), high evapotranspiration (Boldrin et al., 2017) and soil water depletion rates (Carter et al., 2018), Scotch broom is capable of high soil water capture and usage and is a strong competitor for soil water resources

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(Richardson et al., 2002; Watt et al., 2003a). At the same time, Scotch broom possesses several traits that make it tolerant and avoidant of drought conditions, including indeterminant growth, early- and late-season soil water use, large root length density, low leaf area to root mass ratio, high stomatal density in the epidermis, delayed periderm formation, palisade parenchyma with highly developed intercellular airspaces in the outermost regions of the cortex, low specific leaf area, photosynthetic stems, and a drought-deciduous phenology (Bannister, 1986; Bossard and Rejmanek, 1992, 1994; Matías et al., 2012; Boldrin et al., 2017; Carter et al., 2018). Although Scotch broom has developed physiological adaptations that make it a strong competitor on an array of different sites, these traits make it particularly competitive on poor-quality sites with coarsely textured, well-drained soils (Watt et al., 2003b).

Scotch broom is a N-fixing shrub and its physiology and growth may be limited by edaphic factors due to the influence of soil water status and nutrient availabilities on the legume-Rhizobium symbiosis (Carter et al., 2019). Bhuvaneswari et al. (1981) found that *Rhizobia* are unable to infect hosts when water stress prevents active root hair growth – the infection site for *Rhizobia*. Similarly, because of the metabolic costs of forming a symbiosis with *Rhizobia*, N-fixing plants will actively down-regulate nodulation under stress conditions. In general, N-fixing plants have higher nutrient demands than non-fixers; specifically, they have been found to require greater amounts of C, Mg, P, S, and, due to the requirements of the N-fixing enzyme nitrogenase, Mo and Fe (Evans et al., 1993; Barron et al., 2009; Vitousek et al., 2013). Conversely, Sprent et al. (1988) found that when soil N is abundant, N-fixing plants will down-regulate N-fixation and preferentially acquire N from the soil.

Coast Douglas-fir is considered well-adapted to the environmental conditions in the western PNW. Stomatal conductance, however, can vary with soil water availability, generally in order to reduce evaporative losses during periods of drought (Bower et al., 2005). The needle-leafed Douglas-fir can reduce heat exchange resistance, relative to broadleaved species, allowing leaves to remain closer to ambient temperature and reducing evaporative demands during the summer months (Gates, 1968). Roberts et al. (2005) found that under adequate soil moisture conditions, available N and soil temperature can greatly influence growth of Douglas-fir seedlings. Greater N availability has also been shown to enhance stomatal control, reducing unproductive water losses and increasing water-use efficiency (Brueck, 2008).

The contrasting ecologies of ruderal Scotch broom and long-lived Douglas-fir may result in species-specific sensitivities to resource availabilities. Previous studies of Scotch broom on harvested forest sites in the western PNW have demonstrated that, once established, the likelihood of Scotch broom overtopping Douglas-fir seedlings is greater on poor quality sites (Harrington and Schoenholtz, 2010; Harrington et al., 2018). The degree to which the competitive advantages of Scotch broom over Douglas-fir seedlings is mediated by resource availability has not been examined despite that these species often co-occur on recently disturbed sites across the western PNW. In this controlled study, we directly varied resource availability – nutrients and soil water – via fertilization and irrigation in a 2^3 factorial designed to observe the interaction of these variables in relation to the physiology and growth of these two species over two years. This study aimed to understand the functioning and growth of individual Scotch broom and Douglas-fir seedlings in response to varying resource availability in order to broadly explain site-level outcomes. We expected (*i*) the rapid growth rate of Scotch broom to coincide with high soil water depletion relative to Douglas-fir. Douglas-fir, we anticipated, will demonstrate a more conservative ecology with lower soil water use and greater water-use efficiency. We also expected (*ii*) irrigation to have a greater influence on carbon assimilation and growth of Scotch broom and Douglas-fir than fertilization and (*iii*) Douglas-fir height growth to surpass that of Scotch broom under the fertilized-and-irrigated treatment.

2. Methods

2.1. Study site

This study was conducted on a 0.2 ha block at the Washington State Department of Natural Resources' Webster Forest Nursery in Olympia, WA, USA over the course of two growing seasons. The soil at this site is a mesic Aquic Xeropsamment – a deep, moderately well-drained loamy sand of the Cagey series that formed in sandy, glacial drift (Soil Survey Staff, 2017). The local climate is Mediterranean with a winter rainy season and droughty periods in the summer (often > 2 mo), with coastal fog commonly persisting until late morning. Average annual precipitation is 1,469 mm yr^{-1} (2012–2017) and average monthly precipitation during the growing season (April-September) is 101, 59, 32, 9, 27, and 68 mm, respectively. Annual precipitation during the study period was 1478 mm in 2016 and 1659 mm in 2017. Precipitation during the growing season months (April-September) in 2016 was 45, 6, 37, 18, 16, and 56 mm respectively, with relatively dry conditions in April and May. In 2017, precipitation during the growing season months was 147, 88, 39, 2, 4, and 36 mm, respectively (WSU AgWeatherNet – Tumwater SW).

The field used in this study had been left fallow for several years prior to study initiation. Despite not having received fertilization treatments over that time, sufficient levels of most nutrients were found in the soil, while potassium and magnesium levels were low (Table 1; Anderson et al., 2010).

2.2. Study design

Using a completely randomized 2^3 factorial design, 92 4 m^2 plots were randomly assigned to one of the following eight treatment combinations: (1) species (Douglas-fir or Scotch broom), (2) irrigation (present or absent), and (3) fertilization (present or absent). Ten additional plots were randomly assigned to remain untreated to serve as a reference for soil water content measurements (discussed later). In April of 2016, 1 + 1 Douglas-fir seedlings (purchased from Webster Forest Nursery) and 1-year old Scotch broom seedlings of uniform height (transplanted from a nearby clearcut) were planted in randomly assigned plots.

An initial herbicide treatment was applied to the study area as site preparation, followed by treatments to control vegetation in and around each of the plots as needed throughout the study period. Weeds within 1 m of the focal plants were removed manually to avoid

Table 1
Pre-treatment soil nutrient characteristics and properties of the site.

Characteristic or Property	Mean (± SE)
Nutrients (mg kg^{-1})[a]	
Calcium	604 (29)
Copper	1.0 (0.1)
Iron	113 (3)
Potassium	111 (2)
Magnesium	43 (2)
Manganese	12 (0.1)
Sodium	31 (3)
Phosphorus	71 (3)
Zinc	4 (0.1)
Structure[b]	
Bulk density 0–15 cm (Mg m^{-3})	1.48 (0.28)
Bulk density 15–30 cm (Mg m^{-3})	1.43 (0.26)
Coarse fragment 0–15 cm (%)	8.5 (3.3)
Coarse fragment 15–30 cm (%)	9.4 (7.2)

[a] Mehlich extraction (Mehlich, 1984) followed by ICP-AES. All estimates are reported on an oven dry (105 °C) basis.

[b] Bulk density was estimated using the sand-funnel method (Blake and Hartge, 1986).

damaging the planted Douglas-fir and Scotch broom.

The irrigated treatments were supplied water from the resident irrigation system installed at the Webster Forest Nursery and directed to individual plants using plastic irrigation tubing with variable-flow emitters attached at the end of the tubes. Soil water was supplied at a rate of 700 mL per minute for an hour and a half daily from mid-April to mid-June. From mid-June to late-September, the irrigation schedule switched to every other day for a two- to three-hour timespan. In October, the supply of water via irrigation was reduced to nearly zero.

Scotch broom and Douglas-fir seedlings under fertilized treatments were initially fertilized with 100 mL of an 18.2 g/3.8 L H_2O solution of Technigro 20-18-18 fertilizer (equivalent to 962 ppm N) with micronutrients on a weekly basis from April through September. This rate was increased in equal increments of 18.2 g of fertilizer four times starting in August of 2016 on an approximately bi-monthly basis during the growing season to match the presumed increase in nutrient demands of the plants as they grew over the two-year duration of the study. This resulted in a total of 12.3 g of N applied per plant over the course of the two-year (2016: 3.2 g of N per plant; 2017: 9.1 g of N per plant) study.

2.3. Soil water measurements

Soil moisture sensors (model EC-5, METER Group, Inc., Pullman WA, USA) were installed on a randomly-selected subset of plots (n = 40; 5 in each of the 8 treatments) horizontally at 30 cm depth at plot center. Volumetric soil water content (SWC) was measured at an hourly interval each day throughout the year with an Em50 data logger (METER Group, Inc., Pullman WA, USA). Calibration equations developed with soil from the nearby Matlock Long-Term Soil Productivity study (Harrington and Schoenholtz, 2010) were used to calculate SWC.

2.4. Physiology and growth measurements

Using a LI-COR 6400XT portable infrared gas analyzer (LI-COR Biosciences, Lincoln NB, USA), the following physiological variables were measured on a random subset of the Scotch broom (n = 16; 4 per treatment) and Douglas-fir plants (n = 16; 4 per treatment): assimilation rate (μmol $CO_2\,m^{-2}\,s^{-1}$), transpiration rate (mmol $H_2O\,m^{-2}\,s^{-1}$), and water-use efficiency (WUE; μmol $CO_2\,m^{-2}\,s^{-1}$·mmol $H_2O\,m^{-2}\,s^{-1}$). An ambient CO_2 concentration of 400 ppm was used for all measurements. PAR values of 500 and 1500 μmol $m^{-2}\,s^{-1}$ in the cuvette were used in the morning and afternoon, respectively, to standardize light intensity. Measurements were taken throughout the growing season (five dates in 2016 and four dates in 2017), once in the morning (0800–1030 h PDT) and again in the afternoon (1300–1530 h PDT). While samples of Douglas-fir filled the leaf chamber, leaf area measurements of sampled portions of Scotch broom were made by processing digital images of the samples in ImageJ software (Rueden et al., 2017). These area measurements were then used to calibrate the physiological measurements.

To quantify soil water availability to the seedlings, pre-dawn (230–430 h PDT) and mid-day (1100–1300 h PDT) measurements of plant water potential (MPa) were taken on the same aforementioned random subset of Scotch broom and Douglas-fir twice in August 2016, once in August 2017 and once in September 2017. A current-year shoot was collected at mid-crown on the south side of each seedling, placed in a plastic bag containing a wet paper towel, and brought immediately to a pressure chamber (PMS Instrument Co., Albany, Oregon). The chamber was gradually filled with nitrogen gas to identify the minimum balance pressure (nearest 0.01 MPa) required to initiate exudation of water from the cut surface of the xylem tissue.

Measurements were taken at frequent intervals throughout the growing season to quantify seedling growth in stem diameter (mm; root collar for Scotch broom; diameter at 15 cm height for Douglas-fir), height (cm), and crown width (cm)—in both the north-south and east-west directions. Geometric mean crown width was calculated using the following equation:

$$GMW = \sqrt{(a^*b)} \tag{1}$$

where *GMW* = geometric mean crown width, a = north-south crown width, and b = east-west crown width.

Crown volume of Scotch broom was calculated using the following equation (Thorne et al., 2002):

$$CV1 = 2/3\pi h(a/2^*b/2) \tag{2}$$

where *CV* = crown volume of Scotch broom (m^3), h = height, a = crown width 1, and b = crown width 2.

Height and average of the two crown widths were converted to canopy volume (m^3) for Douglas-fir using the equation for volume for a cone:

$$CV2 = 1/3\pi r^2 h \tag{3}$$

where *CV2* = crown volume of Douglas-fir (m^3), r = average radius from two crown widths, and h = height.

A ceptometer (model AccuPAR LP-80, METER Group, Inc., Pullman WA, USA) was used to quantify potential PAR as an index of light capture and canopy density among the treatments. Measurements of PAR were taken within two hours of solar noon in July 2017. Hereafter, 'PAR_B' refers to below-canopy PAR expressed as a percentage of the above-canopy reading.

Scotch broom seed pods and the total biomasses of Scotch broom and Douglas-fir were measured. Seed pods were collected, counted, dried (at 65 °C until constant mass was achieved), and weighed in 2017, the second year of the study and only year seed pods were produced. In October 2017, the same subset of Scotch broom and Douglas-fir (n = 32) used in the physiology measurements was harvested. The aboveground biomass was dried (at 65 °C until constant mass was achieved) and weighed to compare aboveground biomass allocation among treatments.

2.5. Analysis

Models predicting SWC, depletion, physiology (assimilation, transpiration, WUE, and plant water potential) and growth metrics (basal diameter, height, canopy width, PAR_B, and biomass (Scotch broom-only: flowers, seed pods; both species: aboveground)) were fit using the gls function in the nlme package (Pinheiro et al., 2015) in R v 3.4.0 (R Core Team, 2017). Data were analyzed using a first-order temporal auto-regressive correlation structure for repeated-measures ANOVAs. Post-hoc comparisons were made using the least squares means (LS means) function in the lsmeans package (Lenth, 2016). All reported means include ± their standard error in parentheses. P-values were adjusted using the Tukey method to avoid spurious results. The $\alpha = 0.1$ given the inherently high variability of some of the variables measured. P-values are included with all test statistics in the Results.

To check the efficacy of the irrigation treatment, the main effects of species, irrigation, and bi-week number and their interactions were used as predictors of SWC in 2016 and 2017, respectively. Year-specific values of maximum soil water content per sensor were used as an additive covariate. This analysis was done independently of an analysis of depletion because quantifying soil water usage in the irrigated treatments over bi-weekly periods, given that the plots were rehydrated by the irrigation, was not possible.

To test for differences in soil water usage among species and fertilization, the main effects of species, fertilization, growing season week number (weeks 20–40; approximately mid-May to early October), and their interactions were used as predictors in predicting depletion, which was calculated by subtracting the weekly maximum SWC from the weekly minimum SWC per sensor within each year. Depletion was then analyzed within-year and pairwise comparisons made within weeks.

To test for differences in physiological function, the main effects of species, fertilization, irrigation, and date and their interactions were

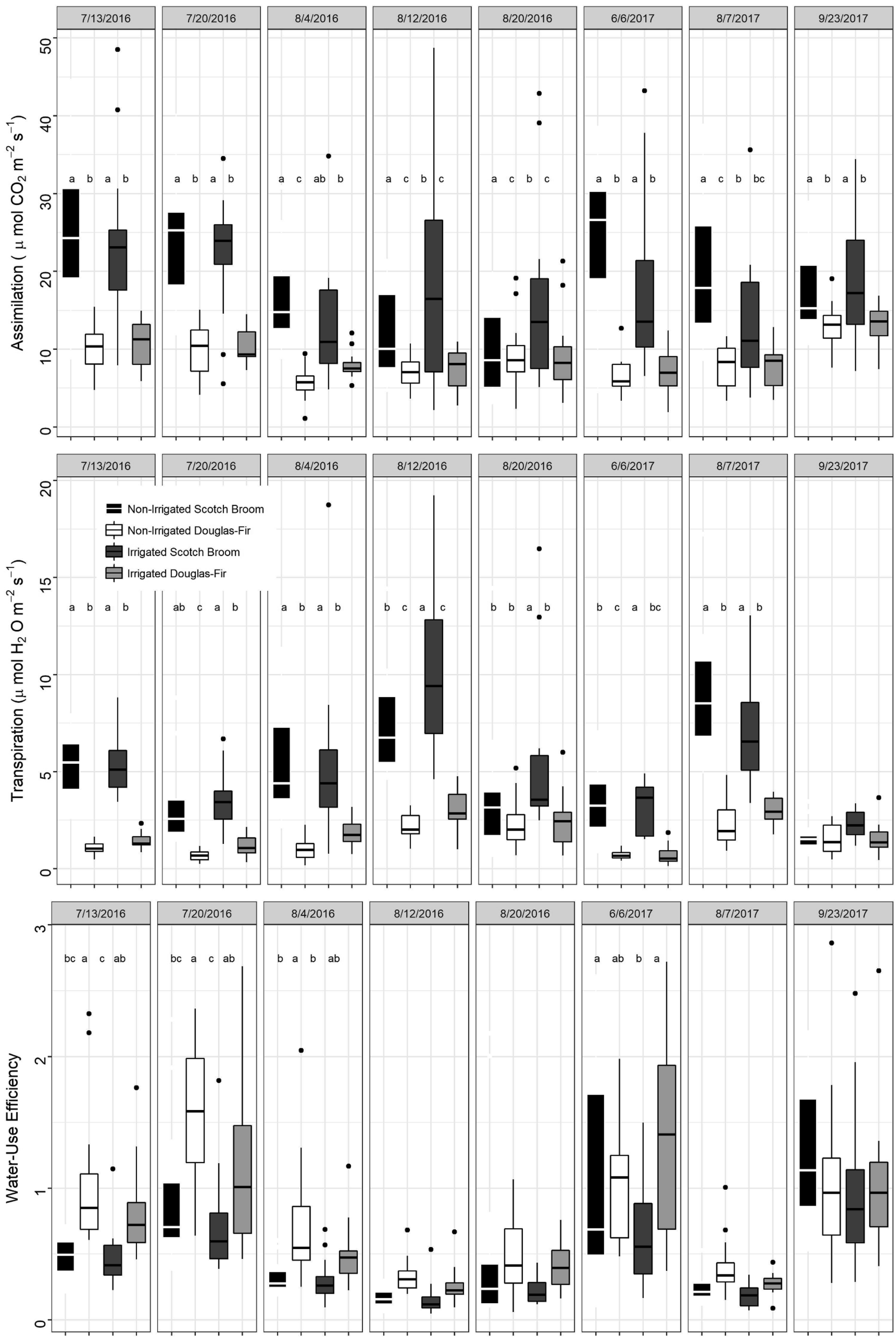

Fig. 1. Physiological measurements of Scotch broom and Douglas-fir between the irrigated and non-irrigated treatments. In box-and-whisker plots, the boxes represent the interquartile range, the median is the horizontal line inside the box, and the whiskers are the highest and lowest observation.

used as predictors for assimilation, transpiration, and water-use efficiency, respectively. Pairwise comparisons were made within dates when significant.

Plant water potential data were pooled to test the effects of species, irrigation, fertilization, and time of day (pre-dawn and mid-day). Absolute values of water potential were log-transformed to meet the assumptions of normality and homoscedasticity. Water potential data were analyzed within-year and pairwise comparisons made within the levels of time of day (pre-dawn and mid-day) when significant.

Species, irrigation, and fertilization and their interactions were used to predict PAR_B. PAR_B was log-transformed to meet assumptions of homoscedasticity and normality.

Growth analyses consisted of two approaches. In the first approach, the approximately bi-weekly measurements of stem diameter, GMW, and height were analyzed within measurement dates. The main effects of species, fertilization, irrigation, and date and their interactions were used as predictors. Pairwise comparisons were made within date when significant. In this approach, diameter, GMW, and height were log-transformed. In the second approach, the stem diameter, GMW, and height growth rates of Scotch broom and Douglas-fir over the two growing seasons were analyzed. Growth rates were calculated by subtracting the initial measurement from the final measurement and dividing that total by two, to account for the two growing seasons. In this approach, the main effects of species, fertilization, and irrigation and their interactions were analyzed. Date was not included in analyses. The intention of the greater temporal resolution of measurements in the first approach was to decipher if differences in the timing of seasonal growth initiation and cessation existed between the two species among treatments. The second approach allowed for investigation into resource-mediated absolute height growth rates and the potential of one species to overtop the other given different growing conditions.

Regression equations for predicting biomass were of the form of the allometric equation $\ln Y = \ln a + b_1 \ln X_1 \ldots + b_n \ln X_n$, where Y is aboveground biomass (grams), X is a size parameter, and ln is the natural log to the base e. Residual analyses indicated that a linear model was appropriate and assumptions were met. Models were constructed with species-pooled and for Scotch broom and Douglas-fir individually. Diameter, height, GMW, and CV1 and CV2 were included in regression models to predict biomass. The best approximating models were selected using Akaike Information Criterion (AIC).

3. Results

3.1. Soil water content

As intended, the SWC in the irrigation treatment was significantly greater than the non-irrigated treatment over the two growing seasons (data not shown). The irrigated treatment had significantly greater SWC than the non-irrigated treatment for all bi-weekly periods in 2016 except the last period ($t = 1.3$; $p = 0.17$). The average difference between the irrigated and non-irrigated treatments throughout 2016 was $0.04 \pm 0.01\ m^3\ m^{-3}$. In 2017, the irrigated treatment had significantly greater SWC than the non-irrigated treatment for all bi-weekly periods except for the second period ($t = -1.4$; $p = 0.17$). The average difference between the irrigated and non-irrigated treatments in 2017 was similar to 2016 at $0.05 \pm 0.001\ m^3\ m^{-3}$.

3.2. Depletion

In comparing the Douglas-fir and Scotch broom in the control and fertilized-only treatments, we found, in 2016, species ($F = 4.2$; $p = 0.04$) and fertilization ($F = 3.5$; $p = 0.06$) were significant in predicting SWC depletion. Douglas-fir had greater depletion than Scotch broom (estimate $= 0.002 \pm 0.001\ m^3\ m^{-3}$; $t = 2.2$; $p = 0.03$) and the non-fertilized treatment had greater depletion than the fertilization treatment (estimate $= 0.002 \pm 0.001\ m^3\ m^{-3}$; $t = 1.9$; $p = 0.06$). In 2017, week was the only significant predictor of depletion ($F = 25.8$; $p < 0.001$). In general, depletion decreased over the growing season and increased abruptly for the final three weeks.

3.3. Physiology

Measurements taken on May 21, 2017 were highly variable, possibly due to instrument error. These data were removed from analysis. The species × irrigation × date interaction was significant in predicting assimilation ($F = 2.5$; $p = 0.01$; Fig. 1). There was no effect of irrigation on Douglas-fir assimilation, while, generally, non-irrigated Scotch broom had the greatest assimilation rates among treatment combinations. Irrigated and non-irrigated Scotch broom assimilation rates were greater than irrigated and non-irrigated Douglas-fir during most of the dates (July 13, 2016, July 20, 2016, June 6, 2017, August 7, 2017 and September 23, 2017). There was a limited effect of irrigation and no effect of fertilization on assimilation.

The species × irrigation × date interaction was significant in predicting transpiration ($F = 3.8$; $p < 0.001$; Fig. 1). Non-irrigated and irrigated Douglas-fir transpiration rates were generally equal and lower than Scotch broom. Irrigated Scotch broom often had the greatest transpiration rate, but occasionally was similar to non-irrigated Scotch broom.

The species × irrigation × date interaction was significant in predicting WUE ($F = 2.1$; $p = 0.05$; Fig. 1). Douglas-fir, regardless of irrigation, often had a greater WUE than Scotch broom. WUE in Scotch broom decreased with irrigation, whereas it remained high in Douglas-fir whether irrigated or not.

In 2016, the species × irrigation × time-of-day interaction was significant in predicting plant water potential ($F = 7.1$; $p = 0.009$). Pre-dawn water potentials were lower (more negative) in non-irrigated Douglas-fir than irrigated and non-irrigated Scotch broom and irrigated Douglas-fir. Mid-day water potentials of irrigated and non-irrigated Douglas-fir were lower than irrigated and non-irrigated Scotch broom.

In 2017, the species × irrigation interaction was significant in predicting plant water potential ($F = 3.9$; $p = 0.05$). Water potentials were lower in non-irrigated Douglas-fir (-1.14 ± 0.15 MPa) than non-irrigated Scotch broom (-0.85 ± 0.12 MPa) and irrigated Douglas-fir (-0.94 ± 0.15 MPa) (data not shown). Time-of-day was also a significant main effect ($F = 426.1$; $p < 0.001$), with mid-day water potentials (-1.6 ± 0.06 MPa) lower than pre-dawn water potentials (-0.27 ± 0.02 MPa). In both years, there was no difference in pre-dawn or mid-day water potential between irrigated and non-irrigated Scotch broom treatments.

3.4. Growth

The species × irrigation × date interaction was significant in predicting stem diameter ($F = 2.2$; $p = 0.004$; Fig. 2). In 2016, non-irrigated Scotch broom had the lowest stem diameter among the species and irrigation treatment combinations. Irrigated and non-irrigated Douglas-fir had the greatest stem diameters for the majority of the 2016 growing season, but this pattern reversed in the 2017 season when Scotch broom had significantly higher diameter growth in both irrigation treatments. In that year, irrigated Scotch broom had significantly greater stem diameter than non-irrigated Scotch broom.

The species × irrigation × fertilization interaction was significant in predicting stem diameter growth rate ($F = 3.6$; $p = 0.06$; Table 2). There were no differences among treatment combinations within species, but treated and untreated Scotch broom had greater stem diameter growth rates than treated and untreated Douglas-fir. The stem diameter growth rates across all treatments of Scotch broom were approximately 163% greater than those of Douglas-fir.

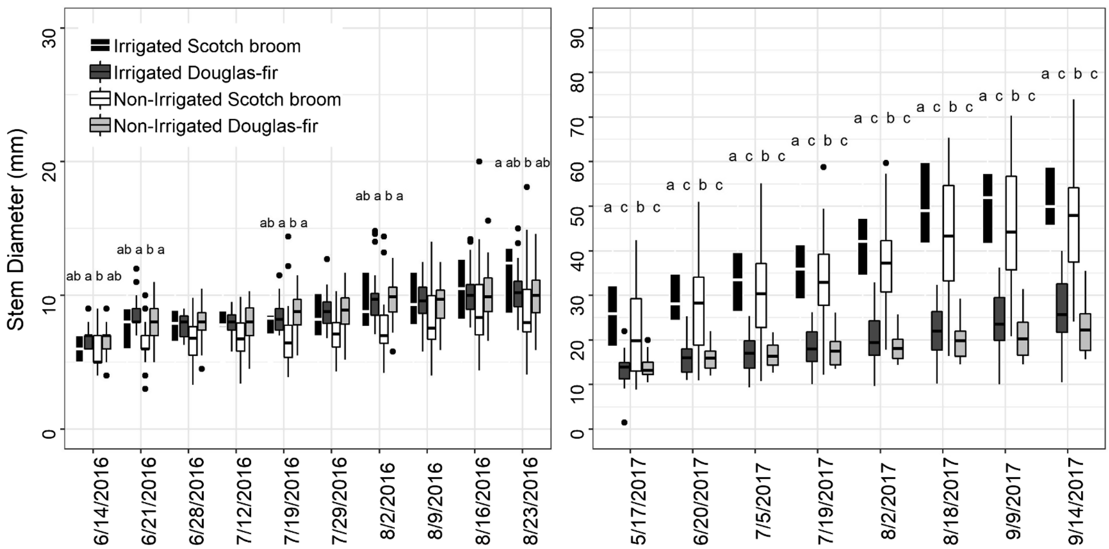

Fig. 2. Back-transformed stem diameter height of Scotch broom and Douglas-fir among the four treatments over the two growing seasons. In box-and-whisker plots, the boxes represent the interquartile range, the median is the horizontal line inside the box, and the whiskers are the highest and lowest observation.

3.5. Geometric mean crown width

The species × date interaction was significant in predicting geometric crown width (GMW) ($F = 52.5$; $p < 0.001$; Fig. 3). Douglas-fir had a significantly greater GMW than Scotch broom in the first years of the study, but GMW of Scotch broom was much greater in the second year with the difference increasing throughout the growing season. In less than one growing season, 1-year-old Scotch broom seedlings had surpassed the GMW of 2-year old Douglas-fir seedlings, regardless of growing conditions.

The fertilization × date interaction was also significant in predicting GMW ($F = 1.8$; $p = 0.02$). No significant differences were detected, however. In general, the GMW of non-fertilized treatments was lower than fertilized treatments in early-2016 and all of 2017, with a period at the end of 2016 where the non-fertilized treatment had greater GMW than the fertilized treatment (data not shown).

Species was the only significant variable predicting GMW growth rate ($F = 371.3$; $p < 0.001$, Table 2). Scotch broom GMW (93.7 ± 3.7 cm yr^{-1}) growth rates were 70.9 ± 3.7 cm yr^{-1} greater than Douglas-fir (23.0 ± 1.2 cm yr^{-1}).

3.6. Height

The species × date interaction was also significant in predicting height ($F = 42.5$; $p < 0.001$; Fig. 3). Treatment effects on height were very similar to those found for GMW. Douglas-fir height was greater than Scotch broom height for all of 2016, but Scotch broom surpassed the height of Douglas-fir early in the growing season of 2017. The mean height differences between Scotch broom and Douglas-fir at the end of the experiment among the four treatments were as follows: control: 77.8 ± 11.3 cm; fertilized: 44.8 ± 12.4 cm; irrigated: 58.0 ± 12.1 cm; fertilized-and-irrigated: 24.4 ± 12.7 cm. The final height of Douglas-fir increased as resources became more abundant; whereas, the final height of Scotch broom decreased as resources became more abundant.

The species × fertilization interaction was significant in predicting height growth rate ($F = 8.8$; $p = 0.004$; Table 2). Similar to stem diameter growth rates, fertilized Scotch broom and Douglas-fir height growth rates did not differ significantly from their conspecific controls. Fertilized and non-fertilized Scotch broom height growth rates, however, were greater than fertilized and non-fertilized Douglas-fir height

Table 2
Growth metric comparisons among species and treatment combinations. Mean ± SE in parentheses. Values with the same letter notation within row are not significantly different. GMW = geometric mean crown width.

Main effects	Scotch broom				Douglas-fir			
GMW growth rate (cm yr^{-1})	93.7 (3.7) A				23.0 (1.2) B			
Spp × Fertilization	Non-Fertilized		Fertilized		Non-Fertilized		Fertilized	
Height growth rate (cm yr^{-1})	83.0 (2.6) A		74.5 (4.2) A		25.5 (2.3) B		35.0 (2.9) B	
Treatments	Control	Fertilized	Irrigated	Fertilized + Irrigated	Control	Fertilized	Irrigated	Irrigated + Fertilized
Stem Diameter Growth Rate (mm yr^{-1})	22.3 (1.6) A	22.5 (2.7) A	27.5 (2.3) A	21.1 (1.9) A	7.4 (0.7) B	8.3 (0.8) B	8.4 (1.1) B	11.5 (1.2) B
Final Diameter (mm)	49.9 (3.4)	50.8 (5.6)	60.7 (4.6)	48.8 (4.0)	21.6 (1.3)	23.1 (1.7)	23.5 (2.2)	30.1 (2.5)
Final GMW (cm)	190.4 (5.8)	191.6 (20.8)	226.8 (13.3)	206.0 (18.3)	70.3 (4.4)	74.3 (4.2)	71.3 (6.4)	84.9 (5.0)
Final Height (cm)	185.2 (8.0)	171.2 (12.8)	179.7 (6.9)	162.2 (10.8)	107.4 (3.9)	126.4 (9.5)	121.7 (8.0)	137.8 (8.4)
Abv. Biomass (g)	3758.1 (481.5) AB	3833.3 (849.9) AB	4790.2 (785.5) A	2232.1 (476.4) B	198.5 (51.0) C	387.7 (95.3) BC	317.7 (71.6) BC	525.9 (36.4) BC
Seed Pod Count	236.3 (108.0) AB	222.5 (73.0) AB	524.0 (188.0) A	52.2 (26.1) B	–	–	–	–
Seed Pod Biomass (g)	10.0 (3.7) AB	12.8 (4.5) AB	23.8 (8.4) A	2.8 (1.1) B	–	–	–	–

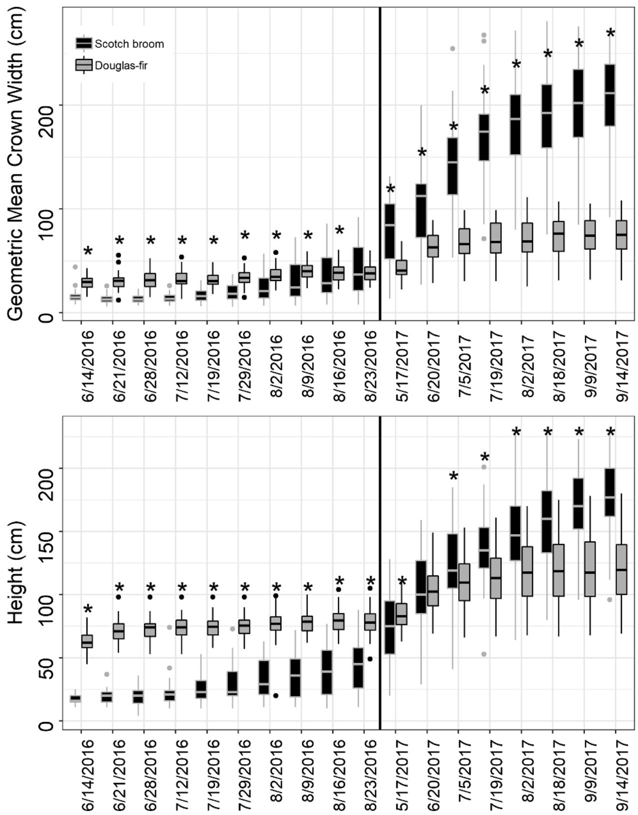

Fig. 3. Geometric mean crown width and height of Scotch broom and Douglas-fir among the four treatments over the two growing seasons. The vertical line separates the 2016 and 2017 growing seasons. In box-and-whisker plots, the boxes represent the interquartile range, the median is the horizontal line inside the box, and the whiskers are the highest and lowest observation.

growth rates. The greatest difference between height growth rates was between the non-fertilized Scotch broom and Douglas-fir (estimate: 57.3 ± 4.2 cm yr^{-1}), while the smallest difference was between the fertilized Scotch broom and Douglas-fir (estimate: 39.4 ± 4.4 cm yr^{-1}).

3.7. PAR_B

The species × irrigation interaction was significant in predicting log-transformed PAR_B ($F = 3.6$; $p = 0.06$). The non-irrigated Douglas-fir (22.7 ± 1.7%) had greater PAR_B than non-irrigated Scotch broom (17.9 ± 2.7%; $t = -2.4$; $p = 0.08$). No other treatment effects on PAR_B were observed ($F < 2.4$; $p > 0.12$).

3.8. Biomass

The species × irrigation × fertilization interaction was significant in predicting biomass ($F = 3.5$; $p = 0.07$; Table 2). Biomass of irrigated, fertilized, and fertilized-and-irrigated Douglas-fir did not differ significantly from that of fertilized-and-irrigated Scotch broom. In all other cases, Scotch broom had greater biomass than Douglas-fir. The only intra-specific difference was irrigated Scotch broom having greater biomass than the fertilized-and-irrigated Scotch broom.

Linear regression equations for Scotch broom and Douglas-fir biomass, combined and individually, showed that stem diameter and CV1 were the two strongest predictor variables (Table 3). An interaction of the natural log of stem diameter and species in a linear model did not yield significantly different slopes between the two species (estimate = -0.006 ± 0.36; $p = 0.99$).

3.9. Scotch broom reproductive tissue

Fertilization × irrigation interaction was significant in predicting both seed pod count ($F = 3.5$; $p = 0.07$) and seed pod dry weight ($F = 3.7$; $p = 0.06$). The irrigated treatment had an order of magnitude greater seed pod count and dry weight than the fertilized-and-irrigated treatment ($t = 2.7$; $p = 0.05$; $t = 2.7$; $p = 0.05$; Table 2).

4. Discussion

The ecologies of Scotch broom and Douglas-fir are quite distinct. Contrasting aspects of the ruderal ecology of Scotch broom versus the conservative ecology of long-lived Douglas-fir were manifested in many of the species' responses to resource availability observed in this study. Investigating the physiology and growth comparisons of these two species at this specific ontogenetic stage in response to different resource availabilities is critical to understanding the susceptibility of recently established Douglas-fir forests of varying soil resource conditions to invasion and dominance by Scotch broom. Douglas-fir remained more competitive with Scotch broom, in terms of height growth, under greater resource abundance in this study, demonstrating a greater site-sensitivity for Douglas-fir seedlings than for Scotch broom.

We expected (*i*) the rapid growth rate of Scotch broom would coincide with high soil water depletion relative to Douglas-fir and that Douglas-fir would be more conservative in its soil water acquisition. Given the continual growth of Scotch broom throughout the growing season, compared to the determinant growth of Douglas-fir, we expected to see some differentiation in the timing of soil water acquisition between the species (Carter et al., 2018). This was not seen in the SWC data, however. Our findings indicate that competition for soil water between these species will coincide during the growing season and likely mediate competitive outcomes at the site-level.

While Douglas-fir generally did show lower transpiration rates and greater WUE than Scotch broom, depletion was greater under Douglas-fir, in some cases. While the latter result may be due to greater evaporative demand, the former results are consistent with the differing ecologies of these two species. Douglas-fir remained more conservative in its use of soil water, as measured by transpiration and WUE, even when soil water was abundant in the irrigation treatment, as the irrigated and non-irrigated Douglas-fir did not differ in terms of transpiration – however, aboveground biomass did differ. This greater WUE of Douglas-fir also did not result in greater plant water potential, which indicates that while this species is utilizing less water, it is also less able to acquire soil water than Scotch broom. In both years, there was no difference in pre-dawn or mid-day water potential between irrigated

Table 3
Highest supported (lowest AIC) allometric equations predicting aboveground biomass (g) of Scotch broom and Douglas-fir seedlings. CV1 is the crown volume equation used for Scotch broom (2/3 π h (a/2 * b/2)); h = height, a = crown width 1, and b = crown width 2).

Species	n	Y	X_1	X_2	*Intercept*	p-value	B_1	p-value	B_2	p-value	R^2
Scotch broom	46	ln Abv biomass (g)	ln stem diameter (mm)	ln CV1 (m^3)	3.4 (1.4)	0.03	1.0 (0.4)	0.02	0.6 (0.2)	0.005	0.71
Douglas-fir	46		ln stem diameter (mm)		0.5 (0.8)	0.56	1.6 (0.2)	< 0.001			0.68
Both	92		ln stem diameter (mm)		−1.9 (0.5)	0.004	2.4 (0.1)	< 0.001			0.88

and non-irrigated Scotch broom treatments. While lower transpiration rates and greater WUE would suggest that there would be more soil water available under Douglas-fir, some physiological or morphological characteristic is presumably limiting the ability of Douglas-fir to access these resources, perhaps in order to avoid drought-induced cavitation of xylem vessels (Kavanagh et al., 1999). Conversely, the large root system of Scotch broom could be physically exploiting a greater volume of soil than Douglas-fir, allowing this species to acquire soil water at a great rate, as evidenced by the irrigated and non-irrigated Scotch broom maintaining similar plant water potentials in both growing seasons. Root length growth has been shown to be inhibited by drought conditions in Douglas-fir relative to more drought-tolerant species (Smit and Driessche, 1992).

Greater soil water depletion under Douglas-fir than Scotch broom was unexpected. Since Scotch broom accrues substantial aboveground biomass, all of which is photosynthetic, and has a greater transpiration rate per unit of leaf area than Douglas-fir, it would follow that soil water depletion would be greater under Scotch broom than Douglas-fir. Instead, the opposite was observed – non-fertilized Douglas-fir had the greatest depletion. A number of factors may have contributed to this. The depth of the soil water sensors and small relative differences in SWC among plots during the peak of the drought, may account for the lack of an expected depletion response. Furthermore, Scotch broom does possess a tap root and may be acquiring soil water from a depth below the 30 cm depth of the sensor (Allen and Allen, 1981), unlike Douglas-fir at this ontogenetic stage. It is possible that this may enable Scotch broom to actively redistribute soil water from greater depths than Douglas-fir; in absolute terms utilizing more soil water but rehydrating the area surrounding the SWC sensor, thus resulting in an underestimate of its total soil water depletion (Dawson, 1993). This dynamic was not revealed in analyses of hourly sensor readings of diurnal SWC but detecting such an effect may require more sensors and higher frequency measurements. Similarly, the greater aboveground biomass accrued by Scotch broom and the resulting lower PAR_B may have created an understory microsite more resistant to atmospheric evaporative demand than that experienced by the less densely foliated Douglas-fir. A similar effect has been measured under shrubs in arid environments (Kidron, 2009). Alternatively, the greater depletion of Douglas-fir in the non-fertilized treatment may be due to lower stomatal control if N was limiting in this treatment. Water-use efficiency was not influenced by fertilization, however, despite N having shown this effect in Douglas-fir seedlings in other studies (Ripullone et al., 2004). It is also important to note that the irrigated Douglas-fir had lower plant water potential than the irrigated and non-irrigated Scotch broom. This would support the hypothesis that Scotch broom's canopy can reduce evaporative demand and or is rehydrating the soil around the sensor by redistributing soil water from greater depths. These mechanisms could allow for greater access to soil water which would then enable the greater growth and lower WUE found in Scotch broom. Clearly, additional work needs to be done to identify soil water usage by these two species at this stage of development.

We expected (*ii*) irrigation would have a greater influence on carbon assimilation and growth of Scotch broom and Douglas-fir than fertilization given the common water limitation to growth in the region (Waring and Franklin, 1979). This expectation was only partially met. Irrigated Scotch broom had a greater assimilation rate than non-irrigated Scotch broom only once (August 12th, 2016). On June 6th, 2017, non-irrigated Scotch broom had a greater assimilation rate than irrigated Scotch broom. On all other dates, assimilation rates of Scotch broom did not differ between treatments. Irrigated and non-irrigated Douglas-fir assimilation rates also never differed significantly. Overall, assimilation rates were greater in Scotch broom than Douglas-fir, often regardless of treatment.

While the initial diameters, GMWs, and heights of Douglas-fir were all greater than Scotch broom at the onset of the experiment, these differences were overcome by Scotch broom by the end of the first or in the middle of the second growing season. It was fertilization, not irrigation, which resulted in greater height growth in Douglas-fir, relative to non-fertilized Douglas-fir. However, unlike Scotch broom which produced less aboveground biomass under the fertilized-and-irrigated treatment than all the other treatments, Douglas-fir accrued greater aboveground biomass in the fertilized-and-irrigated treatment than the Douglas-fir in other treatments. This indicates that Douglas-fir was more sensitive to the limited availabilities of both nutrients and soil water than Scotch broom, a generalist (Potter et al., 2009). This could be the result of the N-fixing ability of Scotch broom enabling growth under conditions in which Douglas-fir would be resource limited. Under the fertilization treatment, Douglas-fir may have allocated resources to greater foliar biomass which in turn enabled greater height growth (Albaugh et al., 1998), and when accompanied by irrigation, ultimately resulted in greater aboveground biomass. It is possible that site quality differentially affects Scotch broom and Douglas-fir growth.

The soil in this experiment was of moderate fertility, compared to the levels found on a high-quality site in Oregon where these species also coexist (Slesak et al., 2016); however, resource limitation presumably contributed to the positive responses to treatment in Douglas-fir, as seen in the other variables like biomass and height growth. Therefore, it could be that the lack of a difference in assimilation was due to rates remaining similar per unit-of-leaf-area and failing to account for an overall increase in leaf area as a result of treatment (Medrano et al., 2015).

Lastly, we expected (*iii*) Douglas-fir height growth would surpass that of Scotch broom under the fertilized-and-irrigated treatment. While fertilized-and-irrigated Douglas-fir did become increasingly competitive with fertilized-and-irrigated Scotch broom, the height growth of Douglas-fir did not surpass that of Scotch broom over the two-year study period. Scotch broom, in part, benefits from an extended growing season, likely starting growth earlier and continuing later into the growing season than Douglas-fir (Carter et al., 2018). Scotch broom was also capable of growing well under all resource conditions. Inexplicably, Scotch broom accrued less height and reproductive and aboveground biomass in the fertilized-and-irrigated treatment than it did in the other treatments; although this difference was only significant compared to the height and reproductive biomass of the Scotch broom in the irrigated treatment. The Scotch broom plants in the fertilized-and-irrigated treatment showed no visual signs of poor health and, although they grew markedly less than the other Scotch broom plants in this study, they still grew to a relatively large size. The plasticity and rapidity of Scotch broom's growth, relative to Douglas-fir's, across a range of resource availabilities justifies early intervention by land managers in controlling this invasive during stand establishment.

5. Conclusion

Overall, this experiment demonstrated that Scotch broom functions and grows at nearly identical rates regardless of resource availability. This indicates a plasticity in Scotch broom that allows it to grow rapidly under varying resource availabilities which is likely what facilitates its competitive advantage on a range of sites. The study also demonstrated that Douglas-fir is more likely to be competitive with the generalist Scotch broom on high quality sites, with greater available soil water and soil nutrients. Furthermore, it demonstrated the potential importance fertilization may play on low to moderate quality sites in increasing the competitive capacity of Douglas-fir. However, the height of Douglas-fir growing under optimized conditions averaged approximately 40 cm less than that of Scotch broom across all conditions by the end of the study – a relatively short time-window, justifying early intervention by land managers to avoid Scotch broom out-competing Douglas-fir seedlings during stand establishment.

Future research involving Scotch broom should investigate the growth and depth of Scotch broom roots, the influence of early- and late-season resource availability on Scotch broom's growth, and an absolute measure of its transpiration. Long-term studies or chronosequences that track the development of Scotch broom and Douglas-fir beyond two growing seasons may be able to note the timing of when Douglas-fir height surpasses that of Scotch broom and the degree to which this timing differs based on site conditions. Ultimately, this may lead to site-specific vegetation control prescriptions that could reduce control costs by prioritizing herbicide treatments on sites highly susceptible to Scotch broom dominance.

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