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Soil texture and other site-level factors differentially affect growth of Scotch broom (*Cytisus scoparius*) and Douglas-fir (*Pseudotsuga menziesii*) seedlings in the western Pacific Northwest

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Abstract: The invasive shrub Scotch broom (*Cytisus scoparius* (L.) Link) is a pervasive threat to regenerating Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) stands in the Pacific Northwest, USA. Field observations indicate that the susceptibility of areas to Scotch broom invasion and dominance can vary by site. We selected 10 sites throughout the western Pacific Northwest that spanned a gradient of soil textures and other factors to test the site-specific susceptibility of Douglas-fir to overtopping by Scotch broom. We expected to find that the ability of Scotch broom to dominate a site was mediated by site-level factors, particularly those influencing soil water — the most limiting factor to growth in the region. We found Scotch broom and Douglas-fir were inversely affected by site-level factors. In general, Douglas-fir absolute height growth rates were more competitive with those of Scotch broom on fine-textured soils than on more coarsely textured soils. We also found Douglas-fir to have a more dramatic response to increasing down woody material than Scotch broom. Scotch broom height growth approached an asymptote at 3 m. Sites with fast-growing Douglas-fir were able to surpass this height 6–7 years after planting and appear likely to avoid suppression by Scotch broom.

Key words: soil water content, depletion, absolute height growth rate, site-specific susceptibility, vegetation management.

Résumé : Le genêt à balais (*Cytisus scoparius* (L.) Link) est un arbuste envahissant qui représente une menace omniprésente pour la régénération des peuplements de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) dans le Nord-Ouest du Pacifique, aux États-Unis. Des observations sur le terrain indiquent que la susceptibilité à l'invasion et à la dominance du genêt à balais peut varier selon la station. Nous avons sélectionné 10 stations dans la partie occidentale de la région du Nord-Ouest du Pacifique de façon à couvrir un gradient de textures du sol et d'autres facteurs pour identifier les facteurs stationnels qui influencent la susceptibilité du douglas de Menzies face à la dominance du genêt à balais. Nous anticipions que la capacité du genêt à balais à dominer une station était influencée par des facteurs stationnels, en particulier ceux qui influencent l'eau du sol qui est le facteur qui limite le plus la croissance dans cette région. Nous avons trouvé que le genêt à balais et le douglas de Menzies étaient inversement influencés par les facteurs stationnels. En général, le taux de croissance en hauteur absolu du douglas de Menzies était plus élevé que celui du genêt à balais sur les sols à texture fine, mais cette différence s'atténuait sur les sols à texture plus grossière. Nous avons également constaté que le douglas de Menzies réagit plus fortement à une augmentation de la quantité de débris ligneux au sol que le genêt à balais. La croissance en hauteur du genêt à balais approchait une valeur asymptotique à 3 m. Sur les stations où il croît rapidement, le douglas de Menzies a pu dépasser cette hauteur 6 à 7 ans après la plantation et semble pouvoir éviter l'oppression exercée par le genêt à balais. [Traduit par la Rédaction]

Mots-clés : teneur en eau du sol, épuisement, taux de croissance en hauteur absolu, susceptibilité spécifique à la station, gestion de la végétation.

Introduction

Evaluating the influence of site factors on the productivity of co-occurring species is important for predicting competitive outcomes across sites, particularly among native and nonnative species. Nonnative species invasion is often associated with disturbances that increase resource availability (Sher and Hyatt 1999). Differences in plant traits among nonnative and native species often mediate establishment success under these conditions (Huang et al. 2016). Traits such as lower constructions costs for plant material (Baruch and Goldstein 1999) and greater photosynthetic capacity

(Funk and Vitousek 2007) and relative growth rate (Burns 2006) are attributed to nonnative species relative to their native competitors. Native species, conversely, generally possess a more conservative strategy with regard to resource use with high resource use efficiency and long-lived tissues (Wright et al. 2004). No one species can be competitive under all site resource availabilities as tradeoffs exist between conservation and acquisition strategies (Reich 2014).

Scotch broom's (*Cytisus scoparius* (L.) Link) generalist, ruderal ecology enables it to thrive as an invasive species around the globe (Potter et al. 2009). Scotch broom is a ubiquitous, nitrogen (N)-fixing invader of early-successional Douglas-fir forests of the

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Pacific Northwest (PNW) and is considered one of the primary competitive species that can lead to Douglas-fir regeneration failures following forest harvesting (Harrington and Schoenholtz 2010). Native to the Mediterranean (Tutin et al. 1968), Scotch broom's climate-of-origin is similar to that of the PNW, thus making it well-adapted to the seasonal fluctuations of precipitation and nutrient limitations in this region (Williams 1981). A prolific producer of seed with 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).

Scotch broom possesses traits that enable it to both acquire limited resources more effectively and reduce its demand for resources during periods of scarcity compared to native species. Scotch broom has been found to be a strong competitor for soil water resources (Richardson 2002; Watt et al. 2003). With a rapid biomass accrual (Fogarty and Facelli 1999), a deep rooting habit (Allen and Allen 1981), and high evapotranspiration (Boldrin et al. 2017), Scotch broom is capable of high soil water capture and usage. At the same time, Scotch broom possesses several traits that make it tolerant and avoidant of drought conditions: high 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). These contrasting traits likely facilitate Scotch broom's ability to thrive in numerous regions around the globe.

The conservative ecology of coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) is considered well-adapted to the environment of the PNW and the dramatic seasonal fluctuations in soil water availability (Gates 1968). The degree and duration of stomatal opening and gas exchange, however, is often limited by soil water availability and increased evaporative demand during the growing season (Waring and Franklin 1979; Bower et al. 2005). At low elevations with no seasonal snowpack accumulation, growth is often negatively related to increasing growing season temperatures and soil moisture depletion (Case and Peterson 2005; Littell et al. 2008). As a result, Douglas-fir wood formation and shoot elongation occurs prior to the onset of the summer drought (Grotta et al. 2005). Under adequate soil moisture conditions, however, available N and soil temperature can greatly influence growth of Douglas-fir seedlings (Roberts et al. 2005). Beedlow et al. (2013) found the effects of temperature and soil water on the growth of Douglas-fir seedlings to be site-dependent.

The climate in the western PNW is typified by cool, wet winters, and dry, drought-prone summers. Less than 10% of the total annual precipitation occurs during the summer months (Waring and Franklin 1979). As a result, soil water is often the most important limiting resource during the growing season (Armson 1979; Brubaker 1980). Plant-available soil water is that which is held in the soil between the permanent wilting point and field capacity. The quantity of plant-available soil water is determined by a number of factors, including soil texture, solar radiation, and precipitation (Armson 1979). These factors are variable across the western PNW.

Concerns over Scotch broom have recently come to the forefront in the PNW. Across the state of Washington, Scotch broom has been deemed to be the most costly invasive plant on forested sites for the state in terms of economic losses (Mefford et al. 2017). Logistical and economic constraints limit the number of hectares in which Scotch broom can feasibly be controlled by landowners, however. There is an urgent need to develop a framework for land managers to assess the susceptibility of Scotch broom dominance at a given site. With this, resource managers could prioritize control efforts and thereby safely reduce costs associated with managing this invasive across their respective land-bases.

Scotch broom's aforementioned physiological adaptations make it a strong competitor of regenerating Douglas-fir on an array of different sites; however, Douglas-fir appears to have the capacity to outgrow and overtop Scotch broom on high-quality sites (Harrington et al. 2018). The degree to which this competitive advantage over regenerating Douglas-fir is mediated by environmental factors has not been examined despite that these species are often co-occurring. To test this, we selected 10 sites in recently harvested coast Douglas-fir forests throughout the western PNW that spanned a gradient in soil textures and presumed soil water availabilities. We expected the growth rates (relative and absolute) of Scotch broom to be relatively constant and greater than Douglas-fir seedlings where soil texture was coarse and soil water availability was low. As soils became increasingly fine textured, however, we expected that the growth rates, specifically the absolute height growth rate, of Douglas-fir regeneration would eventually surpass that of Scotch broom. Our overriding goal is to provide forest managers and landowners with information on the factors influencing Scotch broom's competitive advantage over Douglas-fir during the stand initiation stage and to identify site conditions susceptible to Scotch broom dominance.

Methods

Site characterization

In January of 2016, 10 recently harvested sites were selected that spanned a gradient of soil textures throughout the western PNW. All sites were formerly hand-planted Douglas-fir stands that were 25+ ha in size and were harvested after 2009. The former stands originated between 1929 to 1961 and had been replanted between 2010 and 2016 (Table 1; Fig. 1). Any scattered retained trees and skid trails were avoided when selecting the area to study within each harvested area.

At each site, a centrally located circular 0.1 ha measurement plot (radius = 17.8 m) was identified that represented average site conditions. The first 15 Douglas-fir and 15 Scotch broom plants encountered of high vigor and in open growing conditions (i.e., not in competition with one another) within the plot rotating in a clockwise direction from magnetic north were selected. The result of the systematic selection was a sample of both species of various sizes. A 3 m radius around each selected plant was eradicated of any additional Scotch broom to ensure free-to-grow conditions. Plants were isolated to measure their individual responses to environmental conditions. This facilitated the study of respective traits of each species that were hypothesized to mediate disparate physiological outcomes among sites. While direct competition among the two species is common, this study focused on differences in species-level responses to environmental conditions.

These sites were monitored from January 2016 to January 2019. Sites were characterized by their climate (temperature and rainfall), soil water content, physiography (slope in degrees, aspect in degrees, elevation in metres), soil nutrient and physical properties, time since planting (age), year of stand origin for the recently harvested stand, and downed woody material (DWM) (Table 1).

The local climate was characterized with measurements of air temperature and precipitation using a tipping bucket rain gauge (HOBO model RG3, Onset Corporation, MA, USA) at each site ($n = 1$ per site). Weather data were summarized as mean monthly annual temperature and precipitation and mean monthly temperature and precipitation during the growing season for each site. We defined the growing season to be from 1 May through 31 October (Beedlow et al. 2013). The average percentage of days per year above 4 °C — the minimum temperature at which Scotch broom can photosynthesize (Wheeler 1979) — was also calculated for each site.

Physiographic data were collected using a clinometer, compass, and topographic maps to attain slope, aspect, and elevation, respectively.

Table 1. Site characterization variables among the 10 sites.

	Ascend	Cispus	Deer Creek	Delphi	Dry Bed Creek	Mizzle	Pappy Sorts	RenFair	Sterling	Thin King
Site										
King's site index (m)	39	36	41	37	33	34	33	32	35	38
Stand origin (year)	1947	1961	1961	1953	1951	1946	1937	1940	1929	1955
Planting (year)	2013	2013	2013	2016	2012	2012	2011	2010	2012	2013
Elevation (m a.s.l.)	431	278	290	66	124	126	109	130	194	215
Heat load[a]	−0.24	−0.41	−0.23	−0.40	−0.39	−0.29	−0.45	−0.64	−0.24	−0.26
Climate										
Mean monthly air temp. (°C)	8.8	10.0	10.8	10.5	9.2	10.4	9.4	10.4	10.5	10.8
Mean monthly growing season temp. (°C, May–Oct.)	14.3	14.8	13.3	14.8	13.9	15.3	14.6	14.6	15.2	15.4
Monthly prec. (mm)	217.6	117.3	73.2	127.0	212.0	169.0	134.7	153.5	171.4	119.2
Mean monthly growing season prec. (mm·month^{-1}, May–Oct.)	124.0	82.5	58.7	85.0	111.2	88.6	46.4	78.9	88.1	67.8
Soil physical properties										
Mean monthly soil temp. (°C)	10.7	12.2	10.7	10.7	10.9	11.1	11.4	11.4	11.2	11.9
Min. soil temp.	−3	−3	−3	−4.9	−3	−3	−2.5	−5.8	−3	−3
Days >4 °C (%)	83.0	82.5	86.9	84.0	82.9	88.0	88.2	85.9	87.3	89.1
0–15 cm depth										
Bulk density[b]	0.84	0.83	0.94	1.22	1.04	1.05	0.97	1.25	0.96	0.89
Sand/silt/clay[c]	43/32/25	79/3/18	29/56/15	72/22/6	80/14/6	65/18/17	45/28/27	58/25/17	67/24/9	26/40/34
15–30 cm depth										
Bulk density[b]	0.94	1.03	0.88	1.34	1.21	1.69	1.09	1.16	1.01	1.16
Sand/silt/clay[c]	35/52/13	68/18/14	23/41/36	69/22/9	85/8/7	72/18/10	47/28/25	67/25/9	54/26/20	54/14/32
Forest floor (Mg·ha^{-1})	1.74	1.43	1.55	8.56	7.52	9.96	6.28	3.07	2.97	5.48
Downed woody material (Mg·ha^{-1})[d]										
Small size class	1.2	0.9	1.3	1.2	1.2	1.3	1.3	0	1.2	1.3
Medium size class	3.7	3.7	3.8	3.7	3.7	2.8	3.8	0	3.7	3.7
Large size class	10.4	19.6	2.9	6.0	20.1	10.0	54.7	4.2	49.8	30.5
Total	15.3	24.2	8.0	10.9	25.0	14.1	59.8	4.2	54.7	35.5
Soil chemical properties										
0–15 cm depth										
C (%)	7.4	7.8	5.1	5.7	14.4	8.5	4.9	11.7	8.6	3.7
N (%)	0.3	0.2	0.2	0.2	0.5	0.3	0.2	0.3	0.3	0.2
P (mg·kg^{-1})[e]	1.9	41.1	2.5	5.7	2.9	38.3	3.1	4.3	2.8	2.2
P (mg·kg^{-1})[f]	1.3	86.0	8.3	9.4	5.4	78.0	9.0	10.7	5.1	4.9
Ca (mg·kg^{-1})[f]	775.9	693.1	1018.5	289.5	256.4	937.1	1277.0	613.9	1391.7	1180.0
Mg (mg·kg^{-1})[f]	230.3	146.7	223.9	54.6	58.8	126.3	264.8	109.0	215.2	233.7
K (mg·kg^{-1})[f]	206.4	85.1	205.1	128.1	86.3	96.8	275.1	138.2	273.9	295.0
15–30 cm depth										
C (%)	3.2	3.5	3.4	3.5	5.1	8.1	3.0	7.0	6.1	2.0
N (%)	0.1	0.1	0.2	0.1	0.2	0.2	0.1	0.2	0.2	0.1
P (mg·kg^{-1})[e]	1.4	36.9	1.7	4.3	2.2	34.3	2.8	3.9	1.8	2.4
P (mg·kg^{-1})[f]	0.3	61.1	1.3	2.5	2.9	72.5	5.5	9.1	1.3	0.9
Ca (mg·kg^{-1})[f]	307.3	261.5	605.2	179.3	63.1	514.1	870.1	397.2	1047.7	696.7
Mg (mg·kg^{-1})[f]	150.5	50.2	165.1	34.1	15.3	74.7	215.4	57.9	176.9	167.3
K (mg·kg^{-1})[f]	174.3	48.6	129.7	81.2	42.4	72.0	191.0	74.5	234.1	204.1
Soil water content (SWC)										
Max. SWC (m^3·m^{-3})	0.62	0.58	0.61	0.54	0.40	0.64	0.66	0.59	0.58	0.53
Min. SWC (m^3·m^{-3})	0.05	0.003	0.04	0.06	0.0003	0.05	0.05	0.04	0.09	0.17
Estimated soil water holding capacity (maxSWC – minSWC)	0.57	0.57	0.57	0.48	0.39	0.59	0.61	0.55	0.48	0.36
Mean growing season SWC (May–Oct.) (m^3·m^{-3}·month^{-1})	0.30	0.15	0.24	0.16	0.16	0.12	0.23	0.14	0.17	0.28

Note: a.s.l., above sea level; temp., temperature; prec., precipitation; Min. minimum; Max., maximum.

[a]Heat load was determined using the method from McCune and Keon (2002).

[b]Ascend, Deer Creek, Pappy Sorts, and Thin King were determined using a bulk density core sampler. Cispus, Delphi, Dry Bed Creek, Mizzle, RenFair, and Sterling were determined using the sand funnel method (Blake and Hartge 1986).

[c]Determined with the hydrometer method.

[d]The quantities of downed woody material were determined using the method from Brown (1974).

[e]P was extracted with Bray solution.

[f]P, Ca, Mg, and K were extracted with Mehlich solution.

Fig. 1. Locations for the 10 study sites used in this study. Each dot and associated name correspond to a study site. The Washington state base map was sourced from the State of Washington Department of Ecology (2011). The Oregon state base map was sourced from the USGS (2011). The state boundary polygons were sourced from the US Census Bureau (2020). The geographic coordinate system was GCS North American 1983. [Colour online.]
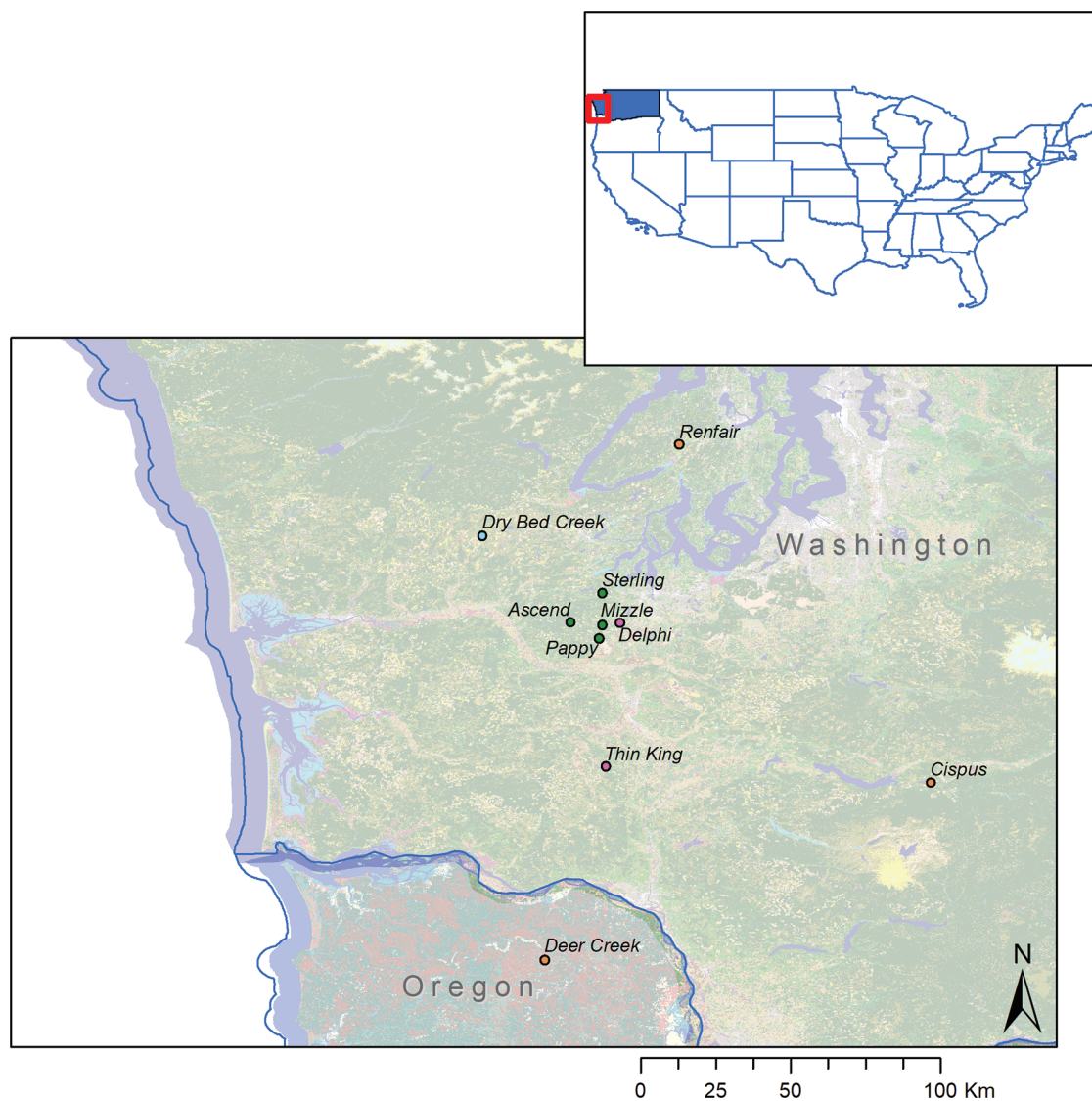
These data were also used to estimate heat load index using the methods of McCune and Keon (2002). The year the recently harvested stand was replanted (henceforth "planting date") was determined by counting the annual internodes of the Douglas-fir and Scotch broom seedlings in addition to using data provided by the landowners. The year the recently harvested stand was planted (henceforth "year of stand origin") was also determined through data provided by the landowners or by counting the annual rings of recently cut stumps if landowners were unable to provide the information.

Volumetric soil water content (SWC; $m^3 \cdot m^{-3}$) was measured on experimental 4 m^2 subplots. We measured SWC under candidate plants (n = 3 Scotch broom and n = 3 Douglas-fir) at each site that were deliberately chosen to span the gradient of plant sizes present at each site. SWC was measured with soil moisture sensors (model EC-5, METER Group, Inc., Pullman, WA, USA) and logged at an hourly interval throughout the year with an Em50 data logger (METER Group, Inc., Pullman, WA, USA). The soil moisture sensors were installed horizontally at a 30 cm depth, 45 cm away

from the stem of each plant in the direction of the data loggers. Each of the Douglas-fir and Scotch broom with SWC sensors, as well as the two non-vegetated plots, had their competitive neighborhood (within the dripline of plant or the entirety of the 4 m^2 plot, whichever was larger) sprayed annually with non-soil active herbicides. The intention of instrumenting an array of conditions with SWC sensors was to provide robust estimates of SWC at each site. Site-level SWC was characterized by summarizing the data as mean monthly growing season SWC, maximum SWC, minimum SWC, and soil water holding capacity (maximum SWC – minimum SWC).

Two vegetated and non-vegetated 4 m^2 subplots were also instrumented with iButton (iButton model DS1921G, Maxim Integrated, San Jose, CA, USA) soil temperature sensors (n = 4/site) installed at a 5 cm depth, which logged soil temperature at 2 h intervals. These data were summarized as mean monthly soil temperatures and minimum soil temperatures among sites.

Bulk density at two depths (0–15 cm and 15–30 cm) was estimated using either a core sampler or the sand funnel method

(Blake and Hartge 1986) depending on soil type. The soil texture — percent sand, silt, and clay — of these same depths at each site was determined using the hydrometer method (Gee and Bauder 1986).

Forest floor mass was estimated using a 0.1 m^2 frame placed 18.8 m from plot center in the four cardinal directions ($n = 4$). All material <0.6 cm in diameter above mineral soil was included in the sample. All samples were mixed in a 5-gallon bucket, transferred to a 3-gallon freezer bag, and brought back to the lab. Once dried (at 65 °C until a constant weight was achieved), these samples were weighed. Mineral soil samples were collected adjacent to the forest floor samples and at the center of the plot at each site at a depth of 0–15 cm and 15–30 cm using a bucket auger. These samples ($n = 4$) were combined into a 5-gallon bucket and mixed thoroughly then placed in a 3-gallon freezer bag. The sample was then brought back to the lab to be air-dried and analyzed. Soil samples were analyzed for total C and N on a 1 g pulverized subsample with dry combustion using a LECO Dumas combustion technique on a Fisons NA1500 NCS Elemental Analyzer (ThermoQuest Italia, Milan, Italy). Phosphorus, Ca, Mg, and K concentrations (mg·kg^{-1}) were determined using Mehlich extraction (Mehlich 1984) followed by ICP-AES (Varian Vista MPX, Varian, Palo Alto, CA, USA). Phosphorus concentrations were also determined using the Bray extraction followed by calorimetric estimation of P on a spectrophotometer (Spectronic 20 Genesys, Model 4001, Thermo Electron Corporation). All estimates are reported on an oven dry (105 °C) basis.

DWM was measured using the methods by Brown (1974). Four 15 m transects per site were oriented along a randomly assigned azimuth. Intersections of fine debris (>0.6 to 2.5 cm; small size-class) within the first 2 m of each transect, intersections of medium debris (>2.5 to 7.5 cm; medium size-class) within the first 4 m of each transect and large debris (>7.5 cm; large size-class) within the entire 15 m length of each transect and its decay class were recorded. Transects were numbered and inventoried starting with the northernmost transect and continued in a clockwise direction. The starting point of each transect alternated from furthest from the center line to closest to the center line to avoid oversampling the center of the plot. DWM measurements were summed and converted to estimates of Mg·ha^{-1} within each size-class and for an estimate of total DWM per site.

Physiology measurements

A subset of the sites that spanned the soil texture gradient (Dry Bed Creek, Mizzle, Sterling, RenFair, Ascend, Thin King, and Deer Creek) were selected for additional physiology measurements. In each of the sites, randomly selected Scotch broom ($n = 8$) and Douglas-fir plants ($n = 8$) were measured for assimilation rates (µmol CO$_2$·m^{-2}·s^{-1}), transpiration rates (mmol H$_2$O·m^{-2}·s^{-1}), and water-use efficiency rates (WUE; µmol CO$_2$·m^{-2}·s^{-1} · mmol H$_2$O·m^{-2}·s^{-1}) using a LICOR 6400XT portable infrared gas analyzer. A CO$_2$ level of 400 ppm was used for all measurements. Measurements were taken twice during the growing season (early- and late-season). Early- and late-season measurements were taken at two different times of the day: once in the morning (0800–1030 h PDT) and again in the afternoon (1300–1530 h PDT). A PAR of 500 (µmol·m^{-2}·s^{-1}) was used in the morning and a PAR of 1500 was used in the afternoon. 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 (Rueden et al. 2017). These measurements were then used to report the physiological measurements on a leaf area unit basis.

Growth

Scotch broom and Douglas-fir growth was assessed with measurements of total height, previous years' height growth (distance from stem base to respective annual internode), height to lowest live crown, and crown width in each cardinal direction. Heights

from previous years along the tallest stem were measured using annual internodes. A qualitative assessment of health and damage was also conducted for each plant. Measurements were taken at study initiation (January 2016) and at the end of the growing season for three consecutive years.

Height to live crown and the two crown widths were converted to canopy volume (m^3) for Scotch broom using the equation from Thorne et al. (2002):

$$(1) \quad CV1 = 2/3\pi h(a/2 \times b/2)$$

where CV is crown volume (m^3), h is height, a is crown width 1, and b is crown width 2.

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

$$(2) \quad CV2 = 1/3\pi r^2 h$$

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

Relative growth rates of crown volume (m^3·m^{-3}·year^{-1}) and height (cm·cm^{-1}·year^{-1}) were calculated using the following equation:

$$(3) \quad RGR = (\ln M2 - \ln M1)/(T2 - T1)$$

where RGR is the relative growth rate expressed as an estimate of proportionate daily growth, T2 time two or the later date, T1 is time one or the earlier date, M2 is the natural logarithm-transformed measurement taken during T2, and M1 is the natural logarithm measurement taken during T1.

Absolute growth rates of crown volume (m^3·year^{-1}) and height (cm·year^{-1}) were calculated using the following equation:

$$(4) \quad ABS = (M2 - M1)/(T2 - T1)$$

where ABS is absolute growth rate, T2 is time two or the later date, T1 is time one or the earlier date, M2 is the measurement taken during T2, and M1 is the measurement taken during T1.

On four sites, the Scotch broom plants used in this study were mistakenly chemically controlled by field crews — Cispus, Sterling, Pappy Sorts, and Ascend — in early 2017. Therefore, height growth monitoring of Scotch broom ceased in 2016. Our ability to utilize the annual internodes to estimate the height growth of previous years on the first inventory, provided sufficient temporal coverage to track growth rates, however.

Analysis

Daily depletion rates under Scotch broom and Douglas-fir plants across sites were calculated by subtracting the daily SWC minimum from the daily SWC maximum. Analyses of these values were focused on depletion rates averaged over the three growing seasons (2016, 2017, and 2018). Site, species, and bi-week were fixed effects and plant identification number nested in year of measurement was used as a random effect in the mixed-effects analysis of covariance (ANCOVA) evaluating depletion. Bi-week was an approximately 14-day period. This length of time was selected to provide fine enough temporal resolution to detect seasonal differences in soil water depletion under the two species.

Mixed-effects ANOVAs predicting physiological measurements (assimilation, transpiration, and WUE) were fit using the lmer function in the lme4 package (Bates et al. 2015). Site and species were fixed effects and plant identification number, time of day (morning or afternoon), and date were the random effects for models predicting assimilation, transpiration, and WUE. Post-hoc comparisons were made using the least squares means (LS means) function in the lsmeans package (Lenth 2016). Comparisons were made within site.

To assess the influence of predictor variables (Table 1) on Douglas-fir and Scotch broom relative and absolute height growth rates, model construction was conducted in four steps. (1) First, the importance of variables in predicting the relative and absolute height growth rates were quantified using the randomForest package in R (Liaw and Wiener 2002; R Core Team 2017), for both species combined and Scotch broom and Douglas-fir individually. (2) The eight predictors (the maximum number of predictors the data would allow) with the highest level of support from the randomForest model (i.e., greatest percent increase in mean squared error = mean of (observed – predicted)^2) when predicting a given response variable were then incorporated into linear mixed-effects models with year of stand origin and planting year as random effects. With the predictor "species" included in the model when assessing species-pooled, the model was tested using a mixed-effects ANCOVA to report the F statistic of the factor and any potential interactions. Models composed of only continuous variables were not tested for interactions. (3) Due to the relatively small sample sizes in this study, models were compared using the Akaike information criterion with a small-sample bias correction (AIC$_c$) using the AIC$_c$ function in the "AICcmodavg" library in R (Burnham and Anderson 2002; Mazerolle 2015). This function was used to determine which model form was best supported by the data, as well as the most parsimonious within a set of models. (4) Lastly, to assess model performance, marginal and conditional R^2 values were calculated using the r.squaredGLMM function in R (Barton 2015). Marginal R^2 values represent the variance explained by fixed factors, and conditional R^2 values represent the variance explained by fixed and random factors. Non-significant variables ($p > 0.1$) were not incorporated into the final models.

Throughout, numerator and denominator degrees of freedom are reported in parentheses with F statistics and all reported means include $\pm$ their standard error in parentheses. p values in multiple comparisons were adjusted using the Tukey method to avoid spurious results.

Results

Physiological parameters

The species $\times$ site interaction was significant in predicting assimilation ($F_{[6,367]} = 3.8$; $p < 0.001$; Fig. 2). Across all sites, Scotch broom assimilation was greater than Douglas-fir. The greatest difference between species occurred on Sterling (estimate: 11.8 ± 2.0 μmol CO$_2 \cdot$m$^{-2} \cdot$s^{-1}; $t = 6.1$; $p < 0.001$). The lowest difference between species occurred on Deer Creek (estimate: 3.4 ± 1.4 μmol CO$_2 \cdot$m$^{-2} \cdot$s^{-1}; $t = 2.4$; $p = 0.01$).

The species $\times$ site interaction was significant in predicting transpiration ($F_{[6,367]} = 20.5$; $p < 0.001$; Fig. 2). Similar to assimilation, Scotch broom transpiration was greater than Douglas-fir across all sites. The species differed the most on Ascend (estimate: 7.2 ± 0.5 mmol H$_2$O$\cdot$m$^{-2} \cdot$s^{-1}; $t = 13.8$; $p < 0.001$) and the least on Dry Bed Creek (estimate: 1.6 ± 0.4 mmol H$_2$O$\cdot$m$^{-2} \cdot$s^{-1}; $t = 4.3$; $p < 0.001$).

Site ($F_{[6,9]} = 1.7$; $p = 0.24$) and site $\times$ species ($F_{[6,367]} = 1.5$; $p = 0.18$; Fig. 2) were not significant in predicting WUE. Only species was significant in predicting WUE ($F_{[1,338]} = 5.3$; $p = 0.02$). Douglas-fir had greater WUE than Scotch broom (estimate: 0.63 ± 0.3; $t = 2.3$; $p = 0.02$).

Soil water depletion

Site $\times$ species $\times$ bi-week was significant in predicting daily soil water depletion over the growing season months ($F_{[231,31\,900]} = 3.6$; $p < 0.001$; Fig. 3). Across all sites, depletion was generally low during the summer drought (0.005 to 0.01 m$^3 \cdot$m$^{-3} \cdot$day^{-1}) and then it increased as the soils started to rehydrate by the end of the growing season, in September and October (0.02 to 0.045 m$^3 \cdot$m$^{-3} \cdot$day^{-1}). Early in the growing season, the depletion rate of Scotch broom surpassed that of Douglas-fir on Mizzle and RenFair in late-May

and early-June by approximately 0.01 to 0.02 (± 0.01) m$^3 \cdot$m$^{-3} \cdot$day^{-1}. Seven of the 10 sites — Cispus, Dry Bed Creek, Mizzle, Pappy Sorts, Ascend, Thin King, and Deer Creek — saw greater depletion under Scotch broom than Douglas-fir, approximately 0.02 ± 0.01 m$^3 \cdot$m$^{-3} \cdot$day^{-1}, in the later part of the growing season, September and October. These differences were occasionally significant for a given bi-week on Mizzle, Pappy Sorts, Ascend, and Thin King. Scotch broom growing on Mizzle nearly sustained a significantly greater depletion rate throughout the growing season.

Relative growth rates

The site $\times$ species interaction was significant in predicting the relative growth rates of crown volume ($F_{[9,280]} = 39.2$; $p < 0.001$) and height ($F_{[9,280]} = 32.5$; $p < 0.001$) (Table 2). Scotch broom generally had significantly greater relative growth rates than Douglas-fir across sites, except for the relative growth rate of Douglas-fir crown volume on Thin King.

Absolute growth rates

The site $\times$ species interaction was significant in predicting the absolute growth rates of canopy volume ($F_{[9,280]} = 16.6$; $p < 0.001$) and height ($F_{[9,280]} = 13.0$; $p < 0.001$) (Table 2; Fig. 4). Scotch broom absolute growth rates among the two metrics were significantly greater than Douglas-fir on four of the 10 sites (Table 2). The absolute height growth rates of Douglas-fir, although not significant, were greater than Scotch broom on Ascend (estimate: 2.6 ± 4.6 cm$\cdot$year^{-1}; $t = -0.55$; $p = 0.60$), RenFair (estimate: 4.6 ± 4.6 cm$\cdot$year^{-1}; $t = -1.02$; $p = 0.31$), and Deer Creek (estimate: 1.9 ± 4.6 cm$\cdot$year^{-1}; $t = -0.41$; $p = 0.68$).
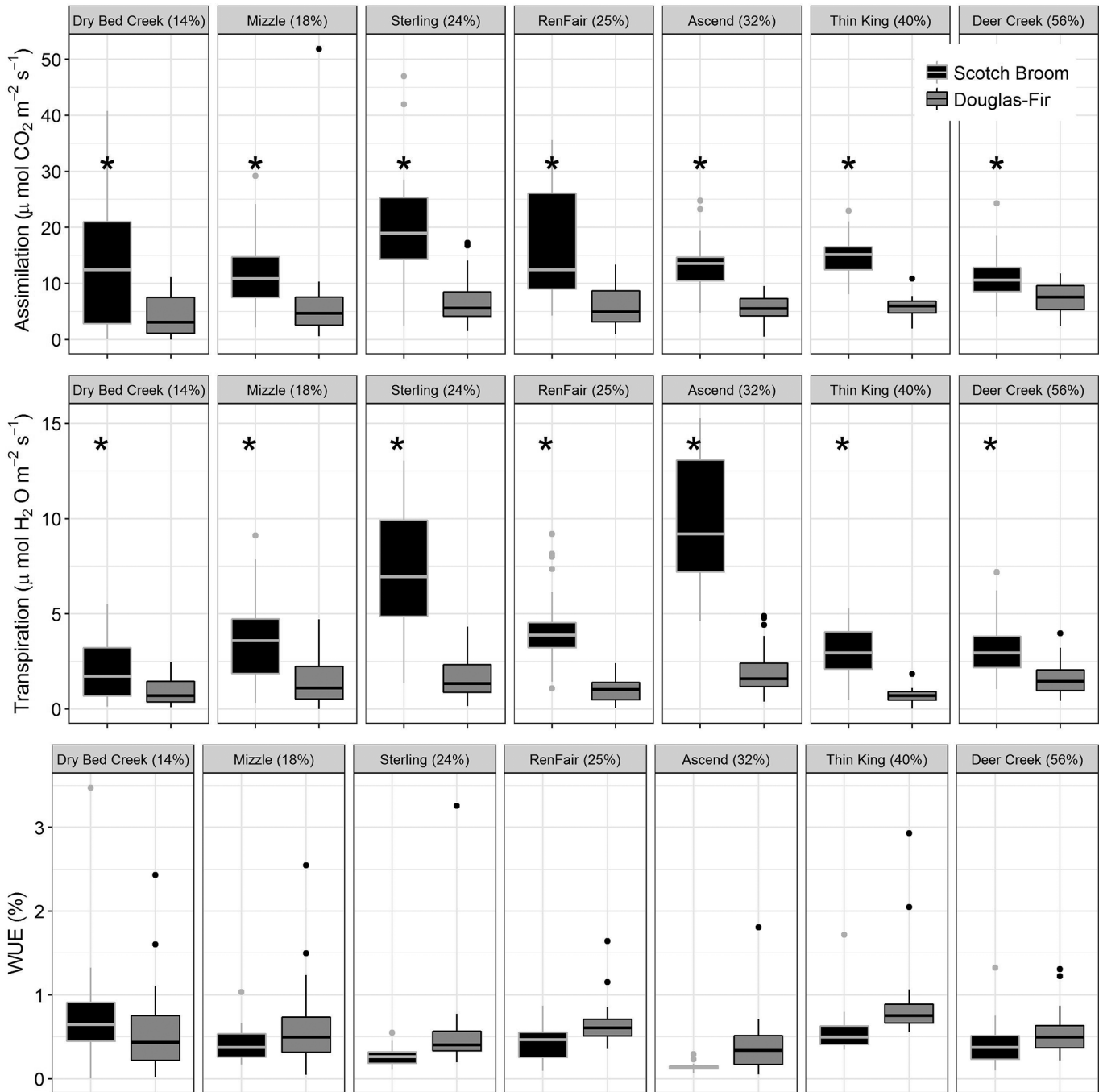
Height growth rate models

The growth rates of both species tended to be associated with soil water content and DWM. However, Douglas-fir and Scotch broom were differentially affected by site-level factors. Douglas-fir absolute height growth rates had greater positive associations with DWM than Scotch broom and the two species responded inversely to the percentage of sand in the soil. The significant variables predicting absolute height growth rates were fairly consistent among the combined species, Scotch broom, and Douglas-fir models (Table 3). Variables associated with soil water (maximum SWC and soil texture) were included in all three models. Each model performed approximately equally with marginal R^2 values of 0.50 for combined species model, 0.49 for the Scotch broom model, and 0.41 for the Douglas-fir model (Table 3).

With the species pooled, the highest supported model included species, bulk density (15–30 cm depth), maximum soil water content and DWM (total). Species was the strongest predictor among the candidate set. Bulk density ($\beta_2 = -21.6 \pm 5.3$; $t = -4.1$; $p < 0.001$) was negatively correlated with absolute height growth rates. Maximum SWC ($\beta_3 = 140.8 \pm 13.3$; $t = 10.6$; $p < 0.001$) and total DWM ($\beta_4 = 0.4 \pm 0.07$; $t = 6.2$; $p < 0.001$) were positively correlated with absolute height growth rates. In the mixed-effects ANCOVAs, the species $\times$ bulk density (15–30 cm depth; $F_{[1,285]} = 22.9$; $p < 0.001$) was significant while the species $\times$ DWM (total) was marginal ($F_{[1,289]} = 3.1$; $p = 0.08$) and species $\times$ maximum SWC was not significant ($F_{[1,279]} = 0.62$; $p = 0.43$). Douglas-fir ($\beta_1 = -53.1$) and Scotch broom ($\beta_1 = -17.7$) both have negative responses to increasing bulk density, but Douglas-fir height growth declines more dramatically than Scotch broom. Douglas-fir had a more dramatic positive response to increasing DWM ($\beta_1 = 0.58$) than Scotch broom did ($\beta_2 = 0.41$) (Fig. 5).

Maximum soil water content (m$^3 \cdot$m^{-3}), percent sand (0–15 cm depth), and bulk density (15–30 cm depth) formed the highest supported model predicting absolute height growth rates of Scotch broom (Table 3). Maximum soil water content ($\beta_1 = 204.7 \pm 33.9$; $t = 6.0$; $p < 0.001$) and percent sand (0–15 cm depth) ($\beta_1 = 0.62 \pm 0.10$; $t = 6.1$; $p < 0.001$) were positively correlated with absolute height growth rates. Conversely, bulk density (15–30 cm

Fig. 2. Assimilation, transpiration, and water-use efficiency (WUE) rates between Scotch broom and Douglas-fir across a subset of seven of the 10 sites used in the study. Asterisks denote significant differences between species within sites. The panels are organized by increasing percent silt in the top 15 cm of the soil profile.

depth) ($\beta_3 = -31.4 \pm 11.7$; $t = -2.7$; $p = 0.03$) was negatively correlated with absolute height growth rates.

DWM (large) and percent sand (15–30 cm depth) forms the highest supported model predicting the absolute height growth rates of Douglas-fir. Large size-class DWM ($\beta_1 = 0.70 \pm 0.2$; $t = 4.5$; $p = 0.004$) was positively related to Douglas-fir absolute height growth while percent sand (15–30 cm depth) was negatively related to its growth ($\beta_2 = -0.42 \pm 0.1$; $t = -4.6$; $p < 0.001$).

In mixed-effects ANCOVAs testing species × soil texture percentages in predicting absolute height growth rates, all species ×

soil texture percentages interactions were significant among all depths (Fig. 6). Douglas-fir absolute height growth rate was positively correlated with increasing percentages of silt and clay at both depths and negatively correlated with increasing percentages of sand. Scotch broom was only negatively correlated with percent silt at the 0–15 cm depth ($\beta_1 = -0.23$) and percent sand at the 15–30 cm depth ($\beta_1 = -0.24$). These relationships were weak, however (adjusted $R^2 = 0.02$ and 0.04, respectively). Over the range of percentages sampled in this study, the absolute growth of Douglas-fir surpasses Scotch broom on sites with high percentages

Fig. 3. Weekly mean soil water content under Scotch broom (n = 3/site) and Douglas-fir (n = 3/site) across the 10 sites over 2016–2018. The panels are organized by increasing percent silt (in parentheses) in the top 15 cm of the soil profile.
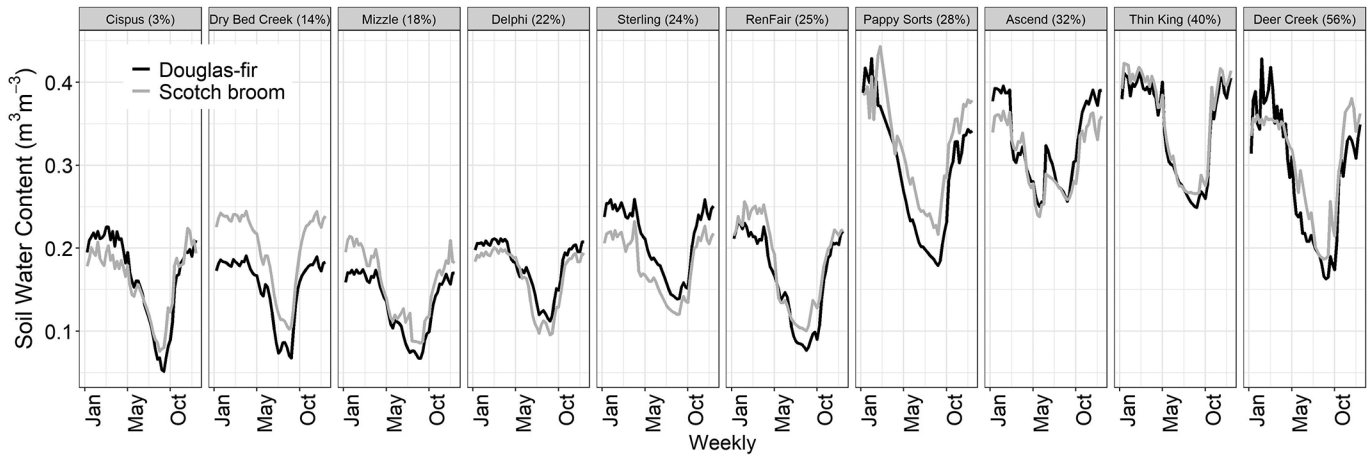

Table 2. Summary table relative and absolute growth rates of the four measured plant attributes among the 10 sites.

	Height[a]		Crown volume[b]	
	Scotch broom	Douglas-fir	Scotch broom	Douglas-fir
Relative growth rates				
Cispus (3%)	**0.67 (0.09)**	0.44 (0.02)	1.51 (0.14)	1.32 (0.04)
Dry Bed Creek (14%)	**0.37 (0.03)**	0.20 (0.01)	0.74 (0.07)	0.58 (0.15)
Mizzle (18%)	**0.49 (0.02)**	0.24 (0.01)	0.86 (0.04)	0.89 (0.04)
Delphi (22%)	**0.70 (0.04)**	0.25 (0.04)	**2.44 (0.19)**	−0.25 (0.12)
Sterling (24%)	**0.63 (0.04)**	0.39 (0.01)	**1.66 (0.23)**	1.02 (0.05)
RenFair (25%)	0.40 (0.02)	0.34 (0.01)	0.68 (0.08)	0.70 (0.03)
Pappy Sorts (28%)	**0.84 (0.06)**	0.48 (0.03)	**2.11 (0.17)**	0.88 (0.02)
Ascend (32%)	**0.53 (0.04)**	0.35 (0.02)	**1.87 (0.13)**	0.89 (0.04)
Thin King (40%)	0.42 (0.04)	0.41 (0.01)	0.73 (0.05)	**1.52 (0.04)**
Deer Creek (56%)	0.37 (0.02)	0.44 (0.01)	0.93 (0.08)	1.08 (0.05)
Absolute growth rates				
Cispus (3%)	**72.0 (0.09)**	42.7 (0.02)	**43.5 (5.6)**	4.01 (0.5)
Dry Bed Creek (14%)	**23.3 (0.03)**	11.3 (0.01)	1.6 (0.3)	0.2 (0.03)
Mizzle (18%)	**49.6 (0.02)**	24.6 (0.01)	**13.0 (1.6)**	1.66 (0.4)
Delphi (22%)	**41.9 (0.03)**	7.3 (0.01)	1.7 (0.3)	−0.01 (0.01)
Sterling (24%)	63.8 (0.04)	56.5 (0.01)	**20.3 (3.0)**	10.0 (1.7)
RenFair (25%)	45.5 (0.02)	50.1 (0.01)	10.9 (2.2)	11.9 (1.7)
Pappy Sorts (28%)	74.8 (0.05)	74.2 (0.03)	13.6 (2.4)	**22.8 (2.0)**
Ascend (32%)	50.5 (0.04)	53.9 (0.02)	16.7 (2.3)	17.4 (2.4)
Thin King (40%)	35.0 (0.04)	**49.5 (0.01)**	8.7 (1.5)	5.3 (1.02)
Deer Creek (56%)	45.7 (0.03)	47.6 (0.01)	**15.4 (2.0)**	8.4 (1.3)

Note: Values are the mean (±SE) of 15 replications per species per site. Bold font denotes significant differences between species within sites. The sites are organized by increasing percent silt (in parentheses) in the top 15 cm of the soil profile.

[a]The unit for height for relative growth rates is cm·cm^{-1}·year^{-1}, and for absolute growth rate it is cm·year^{-1}.

[b]The unit for crown volume for relative growth rates is m^3·m^{-3}·year^{-1}, and for absolute growth rate it is m^3·year^{-1}.

of silt and clay in the soil. The greatest growth discrepancy between Scotch broom and Douglas-fir height growth rates existed on sites with high percentages of silt 0–15 cm in depth.

Discussion

Scotch broom is a pervasive threat to regenerating Douglas-fir stands in the PNW. We expected that the ability for Scotch broom to dominate a site was site-specific and mediated by site-level factors, particularly those influencing soil water — the most limiting factor to growth in the region (Waring and Franklin 1979).

Individual plants compete by tolerating low resource environments (conservative strategy) or rapidly depleting resources to low levels (acquisition strategy) (Goldberg 1990). We expected that the generalist ecology of Scotch broom would result in greater assimilation, transpiration, crown volume, and height growth rates than Douglas-fir regeneration on sites of low quality with coarsely textured soils. However, we expected this competitive advantage to eventually wane, and the growth rates of Douglas-fir would surpass those of Scotch broom as site quality increased. Findings from this study indicate this differential response to site quality between these two often-co-occurring species exists, and that

Fig. 4. Time series of Scotch broom and Douglas-fir height development over the duration of the study. The panels are organized by increasing percent silt (in parentheses) in the top 15 cm of the soil profile.
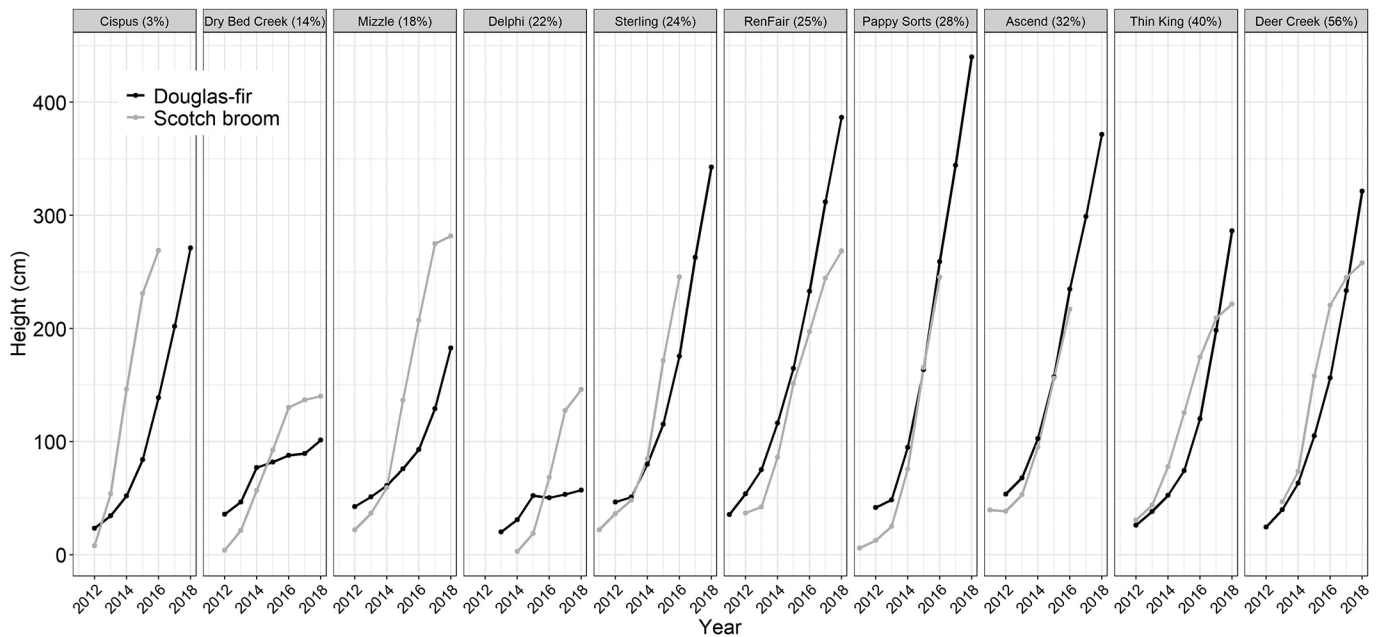

Table 3. Summary table of the highest supported models predicting absolute height growth rates of Scotch broom and Douglas-fir combined and individually.

Response	Species	Model (+ and − represent direction of relationship)	Marginal R^{2a}	Conditional R^{2a}
Absolute height growth rate (cm·year^{-1})	Both	Species – Bulk density 15–30 cm + Maximum soil water content + DWM	0.50	0.54
	Scotch broom	+ Maximum soil water content + Sand 0–15 cm − Bulk density 15–30 cm	0.49	0.58
	Douglas-fir	− Sand 15–30 cm + DWM large	0.41	0.77

Note: DWM, downed woody material.

[a]Marginal R^2 values represent the variance explained by fixed factors and conditional R^2 values represent the variance explained by fixed and random factors.

Douglas-fir will eventually surpass the height growth of Scotch broom on sites with finer texture soils.

The greater transpiration and depletion rates and lower WUE efficiency rates of Scotch broom are consistent with findings from other studies (Carter et al. 2019b). High evapotranspiration rates under Scotch broom were also found by Boldrin et al. (2017). In general, the deep rooting strategies of shrubs are thought to pose a greater competitive risk to crop tree seedlings than other growth forms for belowground resources (Balandier et al. 2006).

Scotch broom's phenological and physiological plasticity likely enable it to photosynthesize and grow earlier and later in the growing season, resulting in greater depletion rates later in the growing season (Carter et al. 2019a, 2019b). Fogarty and Facelli (1999) found that Scotch broom had its highest relative growth rates (mg·g^{-1}·day^{-1}) in the spring and autumn, and a negative relative growth rate during the summer. Bossard and Rejmanek (1992) hypothesized that Scotch broom owes its phenological flexibility and extended growing season to its photosynthetic stems which allow it to maintain a net positive carbon balance throughout the year; presumably to maintain its symbiosis with rhizobia. Our measurement approach was not intended to assess seasonal variation, and it is unclear if seasonal patterns in physiology exist across our sites. Extended leaf phenology and, thus, growing season, is a common trait among invasive plants in forests, however (Fridley 2012).

The trend of increasingly fine textured soils differentially affecting Scotch broom and Douglas-fir was substantiated by patterns in physiology data between species and among sites. Scotch broom had greater assimilation rates than Douglas-fir across all sites that were measured. However, Douglas-fir had its greatest average assimilation rate on Deer Creek (∼9 μmol CO_2·m^{-2}·s^{-1}). While the differences between the two species lessened as percent silt of the 0–15 cm depth increased — as SWC and, presumably, soil water availability increased — Douglas-fir assimilation rates were always significantly lower than Scotch broom. The small physiological differences between the two species on these sites were due to a decreasing assimilation rate in Scotch broom as Douglas-fir assimilation rates remained relatively constant across sites.

Scotch broom height growth remains largely unaffected by soil texture while Douglas-fir responds dramatically. The percentage of finer texture soil particles is likely influencing the soil water holding capacity of the sites as texture is known to be strongly related to soil water characteristics (Saxton et al. 1986). Finer soil particles are likely facilitating these increased growth rates; however, the relationship between estimated soil water holding capacity and percent silt and percent clay was not significant ($p > 0.1$). This is likely a result of our method used to estimate soil water holding capacity, which is less precise than traditional laboratory methods. Average monthly growing season SWC, however, was positively correlated with the percent silt component at the

Fig. 5. Interaction of species × downed woody debris (total) predicting absolute height growth rates of Scotch broom and Douglas-fir. Linear equations predicting absolute height growth rates are presented with Scotch broom placed above Douglas-fir.
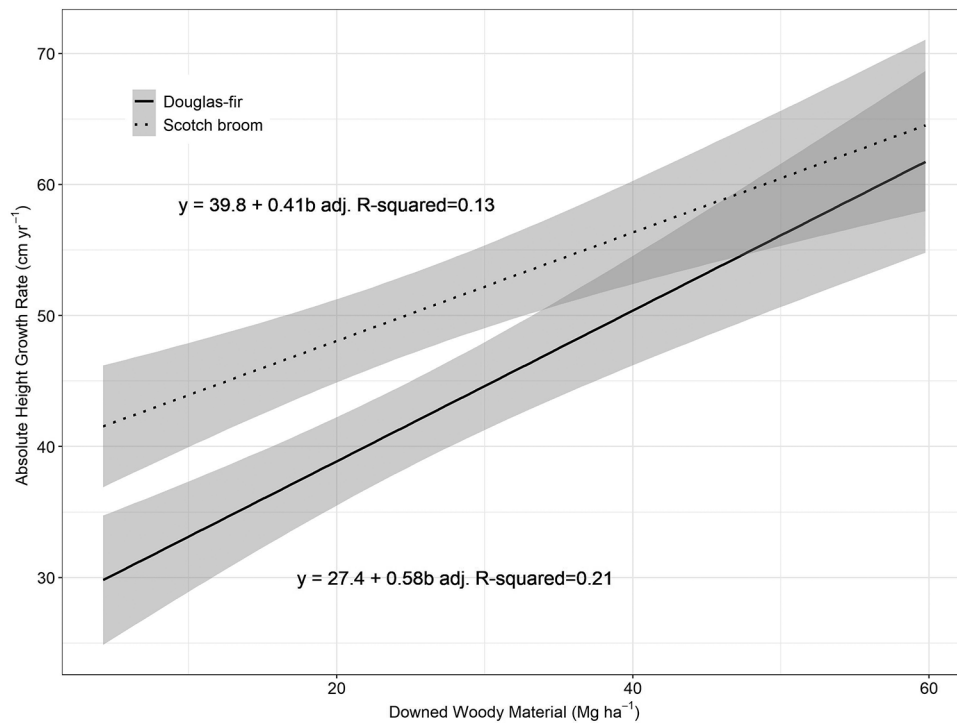
0–15 cm depth ($\beta_1 = 0.003 \pm 0.0002$ m^3 m^{-3}; $t = 15.6$; $p < 0.001$) suggesting greater moisture availability on these sites.

Overtopping of planted seedlings by shrubs post-harvest can lead to high mortality (Balandier et al. 2006). The presence of a continuous layer of 50-cm-tall *Rubus fruticosus* L. was found to completely suppress regenerating *Quercus* seedlings (Frochot et al. 2002). Controlling the shrub *Pteridium aquilinum* (L.) Kuhn measurably improved the growth of *Pinus sylvestris* L. and *Fagus sylvatica* L. in northern Europe where competition was occurring primarily aboveground (Den Ouden 2000). To avoid regeneration failures, it is important seedlings are capable of attaining greater heights than their competitors. The absolute height growth rate of Douglas-fir was significantly greater than Scotch broom on one site (Thin King) and slightly greater on three others (RenFair, Ascend, and Deer Creek) (Table 2). The height growth of Scotch broom begins to asymptote as the species approaches 3 m in height (Fig. 4). This height threshold of Scotch broom may be useful when estimating the susceptibility of Douglas-fir becoming overtopped by Scotch broom. In other words, if Douglas-fir can attain 3 m or more in height before Scotch broom, the risk of being overtopped diminishes. On our relatively fine-textured sites, Douglas-fir was capable of reaching this threshold 6–7 years after planting, similar to Scotch broom on more coarse-textured sites.

These findings corroborate the findings of Harrington and Schoenholtz (2010) and Harrington et al. (2018). On poor-quality sites, with coarsely textured soils that had low water holding capacity, these studies demonstrated that, once established, the likelihood of Scotch broom overtopping Douglas-fir seedlings was high. Harrington and Schoenholtz (2010) showed that Douglas-fir survival was negatively related to Scotch broom cover when it is the dominant competitor on a site following harvest. Douglas-fir mortality during the stand initiation stage of stand development caused large reductions in overall stand productivity of Douglas-fir plantations which were compounded with time since vegetation control (Harrington and Schoenholtz 2010).

Being a generalist, we expected Scotch broom growth rates to remain relatively constant across sites. The decreasing assimilation and growth rates of Scotch broom as site quality increased were unexpected. In general, invasion success is often associated with high nutrient availability (Huang et al. 2016). This finding indicates other factors, besides soil water availability, may be limiting the growth of Scotch broom. While these decreases in assimilation and growth may be the result of more competitive species assemblages interacting with Scotch broom, this effect would likely have been seen in Douglas-fir, as well, if it were present. Furthermore, Scotch broom is considered more competitive than most co-occurring species on these sites. What is perhaps more likely is Scotch broom growth is phosphorus limited. Studies of competition between native and invasive species in low-resource environments tend to focus on nitrogen (Tabassum and Leishman 2016). However, as an N-fixer, the phosphorus demands of Scotch broom are likely greater than those of Douglas-fir (Houlton et al. 2008). Phosphorus (Bray extraction) at the 15–30 cm depth was negatively correlated with percent silt content at the 0–15 cm depth (-0.58 ± 0.04; $t = -12.9$; $p < 0.001$). Slesak et al. (2016) found soil phosphorus was reduced in the presence of Scotch broom over 10 years at a site with relatively low soil N. Caldwell (2006) similarly found high abundances of two soil phosphatases commonly released by legumes under Scotch broom. It is possible that increasing silt content is indicative of sites with an increasing N:P stoichiometry that are not favorable for N-fixation, and thus reduce the competitive advantage of Scotch broom.

Douglas-fir's positive correlation with, and relatively more dramatic response to, DWM in absolute height growth rates provides additional support for retaining coarse woody material (CWM) after forest harvesting (i.e., tree branches and tops) as a form of Scotch broom control. Harrington et al. (2018) found retaining 20 Mg·ha^{-1} of CWM resulted in a 72% reduction in Scotch broom seedling cover compared to that present following conventional whole-tree harvesting (9 Mg·ha^{-1} of CWM retained). The combined positive effects of this treatment — a positive correlation with

Fig. 6. Height growth rates of Scotch broom and Douglas-fir across the two depths of soil textures found in this study. Linear equations predicting absolute height growth rates are presented with Scotch broom placed above Douglas-fir in each figure.
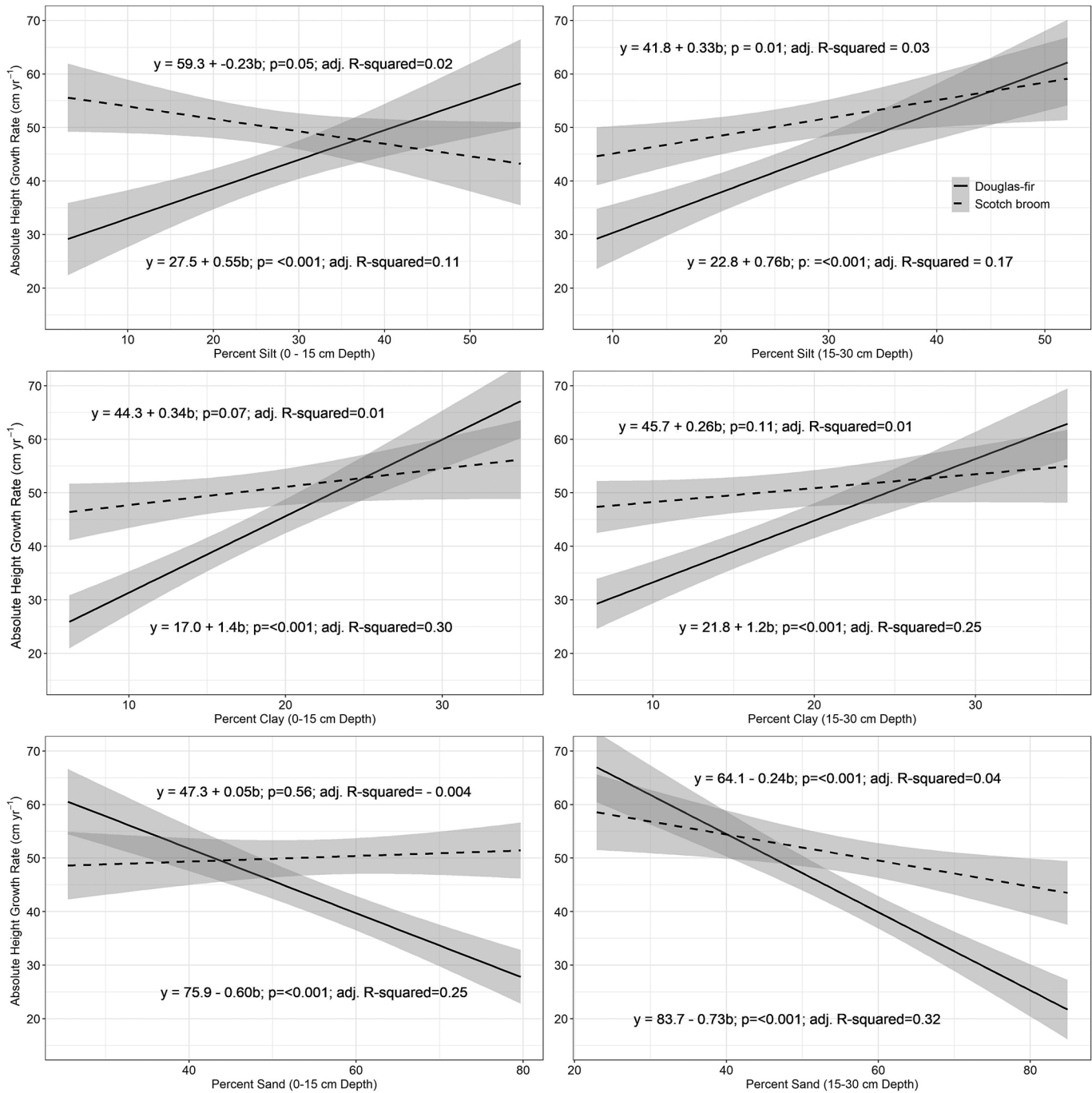
Douglas-fir height growth (found in this study) and decrease in Scotch broom cover ([Harrington et al. 2018](#)) — demonstrate the potential application of this practice in preventing Scotch broom dominance and reducing control costs of this invasive species.

An important factor that was not directly assessed in this study was the density of Scotch broom and its impact on growth. Scotch broom can readily form shrub thickets if left uncontrolled. This study monitored Douglas-fir and Scotch broom that were free to grow. Small, slow-growing Scotch broom can cause regeneration issues for Douglas-fir when densities are high. For example, Delphi was a site that contained a high density of moderately sized Scotch

broom, and the impact of this high density was reflected in the remarkably poor growth of Douglas-fir on this site. Predicting the size of the seedbank of Scotch broom to improve estimates of site-specific susceptibility would be a worthwhile, although challenging endeavor.

Conclusions

These findings, and those from other studies, suggest that the susceptibility of a site to Scotch broom dominance can vary by site and be further mitigated by the retention and dispersal of DWM on the site. Sites with a greater composition of fine

textured soil particles, relatively high soil moisture, and retained logging debris are more favorable to height growth of Douglas-fir seedlings than Scotch broom. These site-level susceptibilities are important for managers needing to prioritize the control of an established, costly invasive species. This framework of detecting site-level susceptibilities by relating regionally important site factors and their influence on height growth could be used in other systems with comparable vegetation control considerations. Notably, many factors, including site index, were not included in any of the models predicting height growth rates. This indicates a potential utility in developing a metric to evaluate height growth potential of Douglas-fir at this early ontogenetic stage of development, which could then be used to infer site-specific susceptibility to Scotch broom dominance. It is important to note that the interplay of regional, climate change driven increases in drought frequency and severity may affect competitive outcomes between these two species. Scotch broom is expected to expand its range toward the poles, globally (Potter et al. 2009), and it may have a greater drought-tolerance than Douglas-fir (Carter et al. 2019*b*).

Acknowledgements

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