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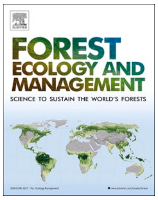

Legacy effects of non-native *Cytisus scoparius* in glacial outwash soils: Potential impacts to forest soil productivity in western Washington

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ABSTRACT

Scotch broom (*Cytisus scoparius* (L.) Link) is a highly competitive, nonnative, leguminous shrub species of major concern in coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) forests of the Pacific Northwest that has potential to impact long-term soil productivity. We conducted a bioassay to assess the potential for legacy effects on soils (e.g., soil nutrient effects, soil seedbank, etc.) following Scotch broom removal and the potential for recovery over time. The bioassay was conducted using glacial-outwash soils from an existing Long-Term Soil Productivity study near Matlock, WA, USA, where Scotch broom had been removed or kept out for 0 (broom present), 4, 10, or 14 years. Soils from each broom removal duration were combined with fertilizer treatments to assess mechanisms of response of three native plant species: yarrow (*Achillea millefolium* L.), Roemer's fescue (Festuca idahoensis Elmer ssp. Roemeri), and coast Douglas-fir. There was evidence for negative soil legacy effects on Douglas-fir growth and biomass, which decreased with time since broom removal. Responses to the fertilizer treatments indicated the effect was not associated with reduced nutrient availability. In contrast, both yarrow and Roemer's fescue had significantly greater biomass in soil from where broom was recently present, which decreased with time since broom removal. Responses to the fertilizer treatments indicated that this positive legacy effect is associated with nutrient availability, likely increased N. Soils from 0 and 4 years since broom removal were estimated as having the potential to produce over 578,500 Scotch broom germinants ha^{-1}. Our results demonstrate the potential for both negative and positive soil legacy effects of broom depending on the responding plant species. Combined effects of negative soil legacies and a large and viable seed bank from Scotch broom create growing conditions likely to hinder long-term productivity of Douglas-fir.

1. Introduction

Scotch broom (*Cytisus scoparius* (L.) Link) is a non-native, invasive leguminous shrub which rapidly dominates recently disturbed sites (Harrington and Schoenholtz, 2010; Richardson et al., 2002; Bossard and Rejmánek, 1994) and alters ecosystem function (Carter et al., 2018, Slesak et al. 2016). The species is currently increasing its range globally with even greater expansion likely under future climate conditions and is a major problem for production forestry in New Zealand, Australia, Canada, and the United States (Potter et al. 2009). In coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) forests of the Pacific Northwest USA, Scotch broom is a species of major concern, causing widespread ecological damage (e.g., native species loss, productivity declines) and significant economic costs (Hulting et al., 2008; CAI, 2017). Scotch broom can proliferate following forest harvesting, especially on low-productivity glacial outwash soils when logging-debris is removed such as in whole-tree harvesting (Harrington and Schoenholtz, 2010). Once established, Scotch broom alters soil properties (Slesak et al., 2016; Grove et al., 2015; Caldwell, 2006), displaces native and promotes nonnative species (Carter et al., 2018), and reduces the growth and survival of Douglas-fir crop trees (Harrington et al., 2018). Impacts to site productivity are large and can last for up to 15 years even when concerted effort is made to control Scotch broom (Harrington et al. 2020). Given the magnitude and potential long-term nature of its impact, there is a need for information to guide forest managers in developing approaches to mitigate the effects of Scotch broom on soil productivity.

One critical information need is to determine if Scotch broom can

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have lasting effects on soil properties and functions after removal (Corbin and D'Antonio, 2011; Weidenhamer and Callaway, 2010). Given its ability to fix moderate quantities of nitrogen (N) (20–100 kg ha^{-1} $year^{-1}$; Carter et al., 2019a, 2019b, Watt et al., 2003), one likely legacy effect is an increase in total and available soil N pools with related effects on site productivity and plant competitive interactions. Studies have found both increases and no change in soil total N in the presence of broom (Shaben and Myers, 2010; Caldwell, 2006), or contrasting responses among soil types (Slesak et al., 2016; Grove et al., 2012). Grove et al. (2015) reported a short-term increase (~1 month) in available N (NH_4 + NO_3) following broom removal, followed by decreased available N at later time periods (up to 22 months post removal). In a different study, Grove et al. (2017) found evidence of increasing N availability (inferred from leaf N concentrations) with increasing duration of invasion (up to 31 years), suggesting that any legacy effect on soil N dynamics would be dependent on the total amount of N inputs via fixation.

Additional N inputs have the potential to alter the availability of other nutrients as well. High levels of nitrate are known to increase cation mobility (Cusack et al., 2016; Smethurst et al., 2001), and can lead to reductions in soil exchangeable pools and soil acidification (Hogberg et al., 2006; Aber et al., 1989). Carter et al. (2018) found higher soil water total N, magnesium (Mg), and calcium (Ca) and lower potassium (K) in plots where broom was experimentally planted relative to non-planted controls. Similarly, Slesak et al. (2016) found lower soil extractable Ca and Mg in the presence of broom, but the effect was only significant at a site with fine textured soil and not apparent at a site with coarse textured soil. Potentially more important are possible effects of increased N on soil phosphorus (P) given the large control over biological activity and known limitations to growth that reduced P availability can exert (Vitousek et al., 2010). Increased P uptake and availability associated with N-fixing species is supported theoretically (Houlton et al., 2008) and empirically (Giardina et al., 1995), and a number of studies have documented lower soil P pools (available and intermediately available) in the presence of Scotch broom (Slesak et al., 2016; Shaben and Myers, 2010; Caldwell, 2006). The effect of lower P pools on the availability of P and related effects on the growth of co-occurring species are unknown. Using a Hedley sequential fractionation procedure to quantify P pools, Slesak et al. (2016) reported no effect of Scotch broom on labile-P 10 years after establishment, but significantly lower intermediately available forms. If Scotch broom causes reductions in soil P, it could impart a legacy effect on plant growth over time.

Scotch broom also has potential to alter plant function via pathways other than altered nutrient dynamics, or indirectly in response to altered nutrient dynamics. Plant species of the genus, *Cytisus*, produce defensive alkaloid compounds with presumed allelopathic effects that have been shown to detrimentally alter functions of some plants (Wink and Twardowski 1992), and these compounds may remain in the soil following Scotch broom removal, potentially impacting growth of associated species (Haubensak and Parker, 2004). Grove et al. (2017) documented reduced ectomycorrhizal fungal (EMF) colonization of Douglas-fir roots in Scotch broom invaded soils, which has also been observed following the addition of Scotch broom litter (Grove et al. 2012). Possible mechanisms leading to reduced EMF colonization include direct suppression of affected plants via allelopathic compounds, or indirect suppression via reduced nutrient availability (Grove et al., 2012; Grove et al., 2017), or competitive exclusion of EMF by arbuscular mycorrhizal fungi.

Legacy effects may also manifest as re-establishment of Scotch broom to a site following its control, via stored seed in the soil. Scotch broom is a prolific producer of seed with multi-year viability (Bossard and Rejmánek 1994). Carter et al., 2019a, 2019b observed that 3-year-old Scotch broom plants produced 26–704 seedpods per year (~30–7800 seeds $plant^{-1}$ at 1–11 seeds pod^{-1}). Estimates from other studies are much higher, ranging from ~ 15,000–40,000 seeds $plant^{-1}$ (Bossard and Rejmánek, 1994; Williams, 1981). Bossard and Rejmánek (1994) estimated that 64% of seeds are likely viable and 40% to 70% of these viable seeds will germinate from a depth of 6 cm or less (Bossard 1993, Williams 1981). This level of seed production can lead to incredibly high levels of Scotch broom germination (e.g., up to 550,000 Scotch broom germinants ha^{-1}; Williams, 1981). Variability in seed production and predation among plants and sites, however, can profoundly influence the total number of germinants. Low to intermediate fires can also increase Scotch broom germination via a heating effect, resulting in a decrease in the species' seed bank compared to unburned areas (Robertson et al. 1999). Nevertheless, there is high potential for a Scotch broom seedbank to grow rapidly, resulting in an extension of the negative soil legacy effect via re-establishment of Scotch broom after attempts are made to control the species (Harrington et al., 2020).

Here we report results from a bioassay that utilized soil with varying durations since Scotch broom removal to assess the potential for long-term legacy impacts to soil productivity including altered nutrient dynamics and seedbank development. To assess altered nutrient dynamics we focused on P limitation, altered nutrient limitation besides P, or other effects not associated with nutrient availability. We tested the following three hypotheses: H_1: Biomass of the bioassay species will be reduced in Scotch broom influenced soils, with the effect becoming less pronounced with increasing time since Scotch broom removal. H_2: Application of P or a complete (N, P, K, Mg, and Ca+ micronutrients) fertilizer will ameliorate effects of Scotch broom on biomass of the bioassay species, with no differences in response between the two fertilizer types (indicating a nutrient limitation is from P alone). H_3: The size of the broom seedbank will decrease with time since Scotch broom removal. Our overall objective was to identify potential soil legacy effects of Scotch broom and the mechanisms associated with them.

2. Materials and methods

2.1. Study site and treatments

A 120-day bioassay was conducted in a greenhouse at the USDA

Table 1
Details of Scotch broom removal durations and associated conditions.

Duration	Description	Removal mode and notes
0-year removal	Broom established in 2003 after forest harvest and present when soils were sampled in 2017	Removal of Scotch broom did not occur. Scotch broom formed a relatively uniform and dense canopy. Area was subjected to operational full tree harvesting conditions in 2003.
4-year removal	Broom established in 2003 after forest harvest, and removed in 2013	Broom plants clipped at 15 cm height and stumps treated with a 20% solution of Garlon® 4 (triclopyr ester) herbicide in oil. Aboveground broom biomass was removed from site. Area was subjected to operational full tree harvesting conditions in 2003.
10-year removal	Broom established in 2003 after forest harvest, and removed in 2007	Broom plants treated with basal stem application of a 20% solution of triclopyr ester in oil. Aboveground biomass retained on the site. Area was subjected to simulated full tree harvesting in 2003 with minimal soil disturbance.
14-year removal	Broom never established after forest harvest in 2003	Area was subjected to simulated bole only tree harvesting in 2003 with minimal soil disturbance.

Table 2

F-statistic probabilities for fixed treatment effects of duration since Scotch broom removal, fertilization, and measurement day on height for each of three bioassay species from a 120-day bioassay of soils from a study site near Matlock, WA, USA. Values in bold are statistically significant ($P \leq 0.05$).

Effect	Num DF	Den DF	Bioassay species		
			Yarrow	Roemer's fescue	Douglas-fir
			Probability > F		
Duration (D)	3	428	0.200	**0.001**	**0.025**
Fertilization (F)	2	428	0.078	**0.034**	0.733
D × F	6	428	0.848	0.270	0.730
Day	8	428	**<0.001**	**<0.001**	**<0.001**
D*Day	24	428	**<0.001**	0.710	0.396
F*Day	19	428	**0.018**	0.856	0.809
D*F*Day	48	428	0.115	0.445	0.543

Forest Service, Forestry Sciences Laboratory in Olympia WA to compare soils having various durations of Scotch broom removal and three fertilizer treatments on growth of three native plant species: yarrow, Roemer's fescue (Festuca idahoensis Elmer ssp. Roemeri), and coast Douglas-fir. The species were selected because of their relevance to management, common occurrence, and to allow for comparisons of response between plant life forms. In early 2018, we identified four areas within a forest site near Matlock, WA, USA that had different durations since Scotch broom removal following its establishment after forest harvesting in 2003. The four removal durations were: 1) 0 years: Scotch broom present since it established from soil-stored seed, 2) 4 years: Scotch broom chemically removed in October 2013, 3) 10 years: Scotch broom chemically removed in July 2007, and 4) 14 years: Scotch broom kept out since 2003. Aboveground Scotch broom biomass was physically removed, and the stumps were sprayed with herbicides in the 4-year removal areas, but the Scotch broom biomass was left in place following chemical treatment for the 10-year removal areas. In both removal durations, a 20% solution of Garlon® 4 (triclopyr ester) herbicide in oil was applied basally to the stem of each Scotch broom plant. Locations for each removal duration were identified based on direct knowledge of previous Scotch broom control efforts at the site (Harrington and Schoenholtz 2010). The forest site is the location of a Long-Term Soil Productivity study affiliate (Harrington et al., 2020), which has closely documented Scotch broom presence and abundance since the study was initiated in 2003, thus we have high confidence that the Scotch broom removal duration locations are accurate. In the 0-year removal duration, Scotch broom density was 2200 stems ha^{-1} (±1300) with crown cover of 31.3% (±17.5). Additional information on the Scotch broom removal durations is presented in Table 1.

Soils at the site are classified as sandy-skeletal, mixed, mesic, Dystric Xerorthents formed in glacial outwash with slopes ranging from 0 to 3% (Soil Survey Staff, USDA-NRCS, 2019). Soil particle size analysis indicated 65, 14, and 21 percent sand, silt, and clay, respectively, and bulk density was 1.45 Mg m^{-3} (Slesak et al., 2016). Soil samples were collected from 10 locations in each removal treatment in March 2018. Sample collection points for each duration were all located within treatment areas of 0.3 ha area or less, and the entire study site encompassed approximately 10 ha. At each soil sample location, the forest floor was removed and then soils were excavated from a 33– x 33-cm area to a depth of 15 cm, which typically encompassed the A horizon. Soils were sieved in the field to remove coarse fragments of 6 mm or greater but to retain existing stored seeds of Scotch broom (i.e., Scotch broom seeds are less than 6 mm across at their widest orientation; USDA, NRCS, 2019). Sieved soils were then composited by duration treatment and returned to the laboratory. Because our research objective was to assess the potential for soil legacy effects following different durations of Scotch broom removal, at the laboratory we thoroughly mixed the soils within each duration treatment to remove microsite effects of the collection sites in order to focus the research on identifying possible soil nutrient or allelopathic mechanisms.

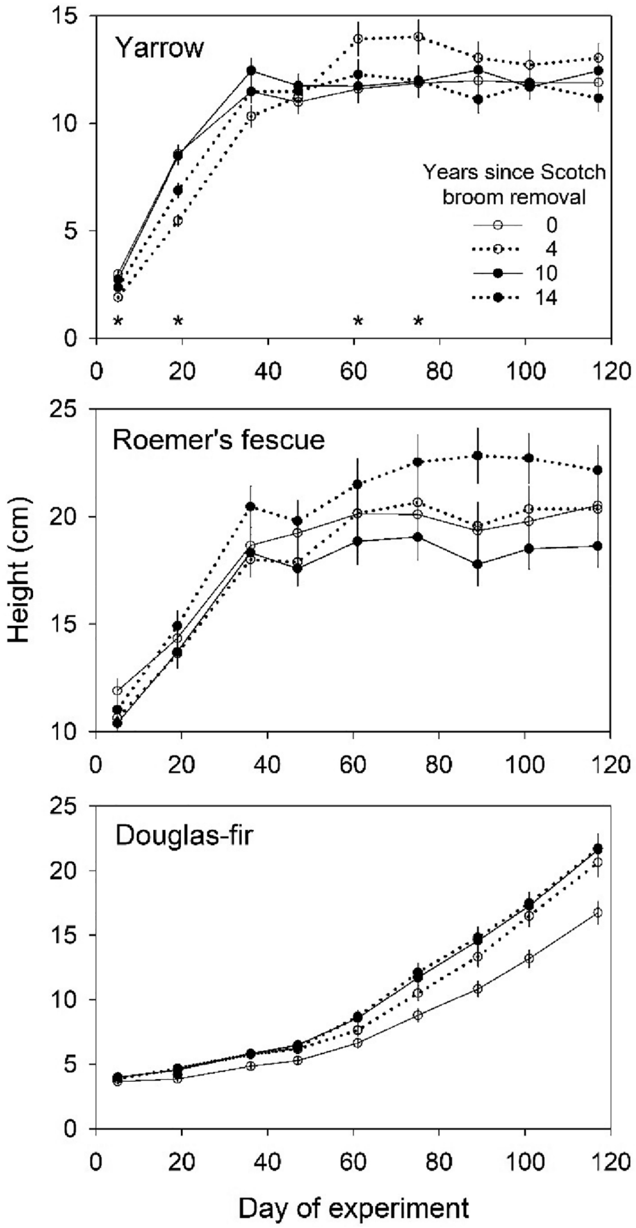

Fig. 1. Average height of yarrow, Roemer's fescue, and Douglas-fir seedlings during a 120-day soil bioassay in response to varying duration since removal of Scotch broom at a study site near Matlock, WA, USA. Asterisks indicate dates in which height for yarrow differed significantly ($P \leq 0.05$) among durations; see text for details on main effect treatment differences for Roemer's fescue and Douglas-fir.

Table 3
F-statistic probabilities for fixed treatment effects of duration since Scotch broom removal and fertilization on aboveground biomass for each of three bioassay species from a 120-day bioassay of soils from a study site near Matlock, WA, USA. Values in bold are statistically significant ($P \leq 0.05$).

			Bioassay species		
			Yarrow	Roemer's fescue	Douglas-fir
Effect	Num DF	Den DF	Probability > F		
Duration (D)	3	44	**<0.001**	**0.009**	0.553
Fertilization (F)	2	44	**<0.001**	**<0.001**	0.308
D × F	6	44	0.065	0.106	0.710

2.2. Greenhouse pot study

We used a complete block factorial experimental design with four durations of Scotch broom removal × three fertilizer treatments that were applied to each of the three species (12 treatment combinations in total for each species). Each of the treatments were replicated five times with blocking according to distance from the greenhouse west-facing wall. Because the soils from each Scotch broom removal duration were composited in the field and mixed in the lab, replicates within a removal duration are actually a form of pseudoreplication that does not represent variance under field conditions (Reinhart and Rinella, 2016). We recognize that this constrains inference of the findings (e.g., magnitude of effects and population variance estimates), but it is an efficient sampling scheme that increases our ability to detect soil legacy effects if they occur by reducing sample variability (Cahill et al., 2017) which has been previously used to assess effects of Scotch broom on soil (Haubensak and Parker, 2004).

For each duration treatment, 2 kg of soil was placed in each of 45, 2.3-L (11.4 cm diameter × 17.5 cm height) pots. Seeds for each bioassay species were collected during late-summer and fall 2017 from the Olympia, WA area. Seedlings were germinated in flats, transplanted into the pots, and grown for 14–21 days prior to initiation of the fertilizer treatments on April 30, 2018. Pots assigned yarrow or Roemer's fescue received three conspecific seedlings each; whereas, those assigned Douglas-fir received only one Douglas-fir seedling because of limitations in numbers of germinated seedlings. Pots were watered as needed with an automated overhead irrigation system.

The three fertilizer treatments included: 1) a non-fertilized control, 2) a one-time P amendment with application of 0.11 g P per pot as triple superphosphate, and 3) bi-weekly application of a complete liquid fertilizer solution (Technigro 20-18-18 plus, Sungro Horticulture, Vancouver B.C., Canada) that resulted in a cumulative-study application of 0.13 g N and 0.12 g P per pot. The selected phosphorus application rates (0.11–0.12 g per pot) represent more than twice the soil concentration observed at the study site (Slesak et al., 2016), and thus, they would likely eliminate P as a growth limiting nutrient. Likewise, the N rate (0.13 g per pot) in the complete treatment was selected to provide a high level of availability for this nutrient to ensure it was not limiting to growth.

Height of the tallest seedling in each pot was measured to the nearest cm every two weeks. During each height measurement, Scotch broom that germinated were counted and removed from each pot to provide an index of the potential number of germinants that the seedbank was capable of producing. At the end of the 120-day study, aboveground biomass was collected from each pot, placed in a paper bag, dried at 65°C to a constant mass, and weighed to the nearest 0.01 g.

2.3. Soils and data analyses

Three soil subsamples were created from the consolidated soils of each removal duration and analyzed for soil chemical characteristics. Total soil C and N were measured 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). Available soil P was estimated using the Bray extraction followed by calorimetric estimation of P on a spectrophotometer (Spectronic 20 Genesys, Model 4001, Thermo Electron Corporation). The Mehlich method (Mehlich 1984) was used to extract soil Ca, Mg, and K. Extract concentrations were measured with inductively coupled plasma spectroscopy (Varian Vista MPX, Varian, Palo Alto, CA, USA). All estimates are reported on an oven dry (105 °C) basis.

All statistical analyses were conducted in SAS (SAS Institute, Inc., 2013) using a significance level of $\alpha = 0.05$, and separate statistical models were run for each species. Height data for each species were subjected to repeated-measures, mixed-effects analysis of variance (ANOVA) to test for fixed effects of Scotch broom removal duration, fertilizer treatments, day of experiment, and their interactions after adjusting for the random effects of blocking. Residuals were plotted against predicted values to check for non-homogeneous variance. When a significant main effect or interaction among main effects was detected, multiple comparisons of treatment means were conducted with Tukey's HSD test to identify dates in which differences existed due to treatment (Sokal and Rohlf, 1981). Bonferroni probabilities were used to judge statistical significance and avoid a Type I error. The same approach (excluding the use of repeated-measures and day of experiment as a fixed effect) was used to analyze aboveground biomass of the bioassay species. Survival of planted seedlings for each species was 100% for the duration of the experiment. For Roemer's fescue and yarrow, total biomass per pot was divided by 3 to estimate average biomass per plant.

To provide an index of potential Scotch broom germinant numbers in each soil treatment, the total area sampled per duration treatment was divided by 45 – the number of pots per treatment – and then converted to hectares to estimate the area from the study site that is represented by each pot. Therefore, the per hectare total of Scotch broom germinants represented by each seedling counted per pot (x) was equal to x/0.00000242. The estimated total number of Scotch broom germinants

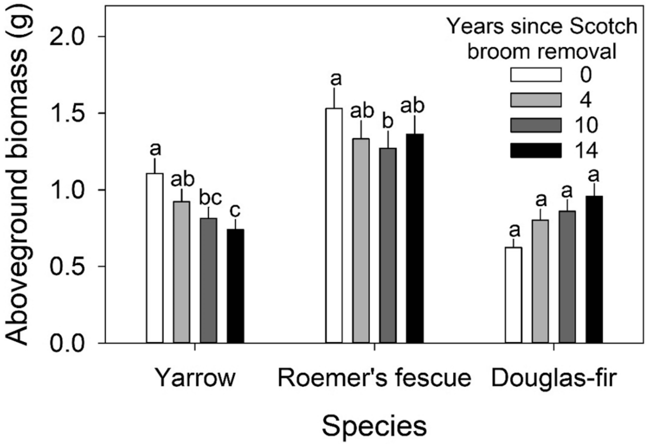

Fig. 2. Average aboveground biomass (with standard error bars) of yarrow, Roemer's fescue, and Douglas-fir in a 120-day soil bioassay in response to varying duration since removal of Scotch broom at a study site near Matlock, WA. For a given species, histograms labeled with the same letter do not differ significantly ($P \leq 0.05$) among durations of Scotch broom removal.

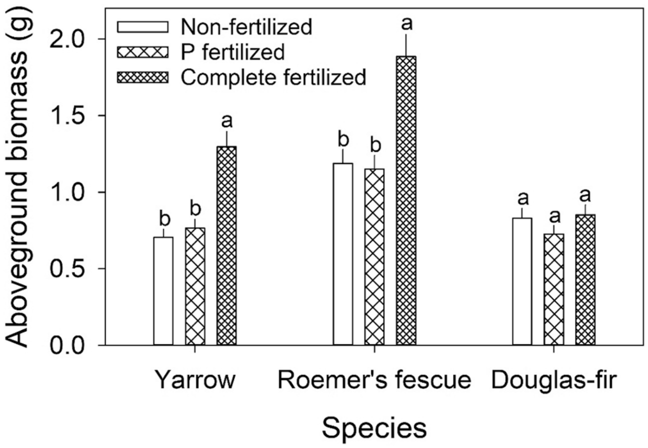

Fig. 3. Average aboveground biomass (with standard error bars) of yarrow, Roemer's fescue, and Douglas-fir in response to three fertilizer treatments applied in a 120-day soil bioassay. For a given species, histograms labeled with the same letter do not differ significantly ($P \leq 0.05$) among fertilizer treatments.

per hectare were subjected to a mixed-effects ANOVA for each bioassay species to test for fixed effects of Scotch broom removal duration, fertilizer treatment, and their interactions after adjusting for the random effects of blocking. Multiple comparisons of treatment means were conducted using the same approach as described previously.

3. Results

3.1. Soil chemical characteristics

Differences in soil chemical properties were variable among the four Scotch broom removal duration treatments (Supp. 1). There was no significant difference in total N concentration among treatments, but C concentration was significantly greater in the 14-year removal duration, resulting in the highest C:N ratio among treatments. Nutrient cation concentrations were generally greatest in the 0- and 10-year duration treatments compared to the 4- and 14-year removal treatments. Total and available P concentrations were significantly lower in the 4-year duration treatment relative to other duration treatments. Taken together, the most consistent effect of duration on soil chemical properties was lower concentrations of C and nutrients in the 4-year duration treatment relative to other durations.

3.2. Height responses

There were either main effects of duration treatment or an interaction between duration and measurement day for each species (Table 2). Yarrow height in the 4-year removal duration was significantly lower than in the 0- and 10-year removal durations early in the bioassay, but significantly greater than all other duration treatments later in the bioassay (Fig. 1). Roemer's fescue height in the 14-year duration (19.3 cm) was significantly greater than in the 4- and 10-year durations (17.5 and 16.7 cm, respectively). Douglas-fir height was significantly lower in the 0-year duration than in the other durations, with treatment differences increasing as the experiment progressed. By the end of the study, Douglas-fir height in the 0-year duration was 16% and 21% less than in the 4- and 14-year removal durations, respectively.

There was a main effect of the fertilization treatment for Roemer's fescue in which height in the complete fertilizer treatment (18.4 cm) was significantly greater than in the P fertilization treatment (17.0 cm), but it did not differ from that in the non-fertilized treatment (18.1 cm). For yarrow, a significant interaction between fertilizer treatment and measurement day was associated with significantly greater height in the complete fertilizer treatment compared to the non-fertilized treatment on measurement days 19 and 61 (data not shown). There was no detectable effect of fertilizer treatment on Douglas-fir height.

3.3. Biomass responses

There were main effects of Scotch broom removal duration and fertilization treatment on aboveground biomass for both yarrow and Roemer's fescue (Table 3). Patterns of response were similar for both species, where biomass was greatest in the 0-year duration (Fig. 2). For yarrow, biomass in the 0-year duration was 33% and 42% greater than in the 10- and 14-year removal durations, respectively, and for Roemer's fescue it was 19% greater than in the 10-year removal duration. There was no significant effect of removal duration on Douglas-fir aboveground biomass, but estimates were lowest in the 0-year removal treatment and consistently increased with increasing removal duration (Fig. 2). Patterns of response to fertilization treatments were also similar for yarrow and Roemer's fescue (Fig. 3), where aboveground biomass was significantly greater with the complete fertilization than either the non-fertilized or P-fertilized treatments (~70% greater with yarrow and ~ 50% greater for Roemer's fescue). There was no effect of fertilization on Douglas-fir aboveground biomass (Fig. 3).

3.4. Scotch broom germination responses

The number of Scotch broom germinants in pots containing Douglas-fir or Roemer's fescue differed significantly among durations of Scotch broom removal ($p \leq 0.017$), but differences were not significant for yarrow ($p = 0.092$) (Table 4; Fig. 4). For the 0- and 4-year removal durations, germinant numbers in pots containing Douglas-fir greatly exceeded those observed for the other two bioassay species (by a factor of 3–4). The total number of germinants declined to zero for each bioassay species in the 10- and 14-year durations. For Roemer's fescue, the number of Scotch broom germinants in the 4-year removal duration was greater than in the 10- and 14-year removal durations (Fig. 4). There was no effect of fertilization on the total number of germinants (Table 4).

Table 4
F-statistic probabilities for fixed treatment effects of duration since Scotch broom removal and fertilization on cumulative number of Scotch broom germinants found under each of three bioassay species from a 120-day bioassay of soils from a study site near Matlock, WA, USA. Values in bold are statistically significant ($P \leq 0.05$).

			Bioassay species		
			Yarrow	Roemer's fescue	Douglas-fir
Effect	Num DF	Den DF	Probability > F		
Duration (D)	3	44	0.092	**0.017**	**<0.001**
Fertilization (F)	2	44	0.498	0.854	0.860
D × F	6	44	0.644	0.0778	0.152

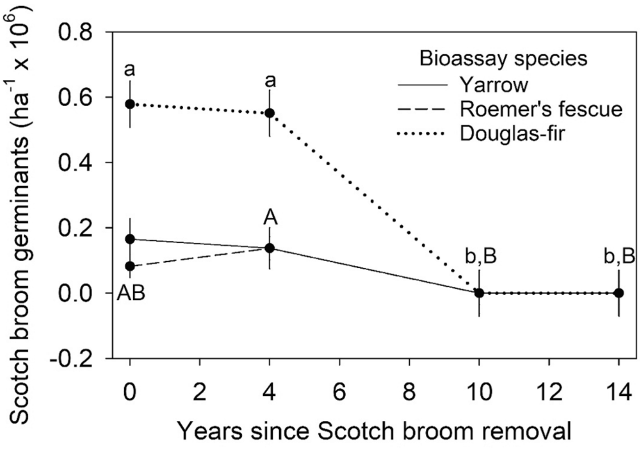

Fig. 4. Average number of Scotch broom germinants estimated from a 120-day soil bioassay that compared growth of three plant species in soils of varying duration since removal of Scotch broom. Lowercase and uppercase letters indicate significant differences ($P \leq 0.05$) for pots containing Douglas-fir and Roemer's fescue, respectively. Scotch broom germinants for pots containing yarrow did not differ significantly among duration treatments ($P = 0.092$).

4. Discussion

Scotch broom is a serious threat to the ecology and functioning of coast Douglas-fir forests, and soil legacy effects have potential to exacerbate impacts of this aggressive invasive species. Results from our bioassay experiment provide evidence that legacy effects do occur, they lessen with time since Scotch broom removal, and their effects on plant growth vary by species. Our results also indicate that Scotch broom germinant numbers are influenced by duration of Scotch broom removal and the species under which germination occurs. These findings have implications for the management of Scotch broom in countries where it is a serious threat to forestry operations including New Zealand, Canada, and the United States (Potter et al. 2009). The findings may also have implications for the management of other problematic N-fixing forest invasive plants, particularly common gorse (*Ulex europaeus*), which has similar characteristics to Scotch broom and occupies similar environments (Clements et al. 2001).

Several studies have documented legacy effects of Scotch broom-influenced-soil on plant growth (Grove et al., 2012; Haubensak and Parker, 2004), and our results provide additional support for this phenomenon. Notably, we measured a significant reduction in Douglas-fir height associated with the 0-year removal treatment and a non-significant trend of increasing aboveground biomass with increasing duration of Scotch broom removal. Grove et al. (2012) attributed the legacy effect to indirect effects of allelopathy on colonization by ectomycorrhizal fungi (EMF), which was lower on Douglas-fir roots grown in Scotch broom invaded soil compared to uninvaded soil. Here, the lack of Douglas-fir response to either of the fertilizer treatments indicates that the negative legacy effect is unrelated to nutrient availability in soil. In particular, there was no evidence of a soil P limitation which we had hypothesized based on previous work (Slesak et al., 2016; Caldwell, 2006; Houlton et al., 2008; Giardina et al., 1995). If reduced colonization by EMF is a primary driver of Scotch broom's soil legacy effect on Douglas-fir, our results suggest that the effect is associated with a mutualistic benefit provided by EMF to the host plant beyond increased nutrient or water acquisition (water was kept at a non-limiting level across all treatments). Regardless of the mechanism, legacy effects on Douglas-fir productivity may include delayed or stunted early growth after planting and a potential for increased competition intensity from herbaceous species due to positive legacy effects of Scotch broom (see below). Both of these phenomena could result in additional Douglas-fir mortality from competing vegetation, impacting long-term site productivity.

The contrasting responses of yarrow and Roemer's fescue compared to Douglas-fir are not surprising as a number of studies have shown species-specific responses using bioassay approaches (Kadeba and Boyle, 1978; Denslow et al., 1987). In the case of yarrow, our observed biomass response contrasts with that of Haubensak and Parker (2004) who found a 30% reduction in yarrow biomass when grown in prairie soil invaded by Scotch broom for 10–15 years. Soils from the 0-year removal duration in our study had been under the influence of Scotch broom for a similar duration, and soil characteristics (texture, C and N pools) were estimated to be similar, as well. It is, therefore, unclear what may be driving the contrasting results between studies. Regardless, the significantly higher biomass values in the 0-year removal duration for both yarrow and Roemer's fescue are likely in response to increased nutrient availability given the positive response to the complete fertilizer treatment. We cannot determine exactly which nutrient(s) caused the response, but it is probably due to increased N availability in Scotch broom-invaded soils (Haubensak and Parker, 2004; Grove et al., 2017). For these species, at least, it appears that Scotch broom has a positive, albeit brief, soil legacy effect on their growth.

For all species, the observed legacy effects diminished with time, indicating that recovery to pre-invasion conditions is likely if control efforts are taken to prevent the reestablishment of broom germinants. Given that most of the effects we observed were associated with the 0-year removal treatment and not significant by the 4-year removal duration, it appears that legacy effects are short-lived and recovery occurs sometime within four years of Scotch broom removal. We temper this conclusion by drawing attention to the fact that aboveground biomass of Scotch broom was removed from the soil sample areas after plants were severed in the 4-year removal treatment, which likely reduced any legacy effect on soil. Carter et al. (2019a, 2019b) found that the vast majority of N fixed by Scotch broom over a two-year period was retained within the plant with little transfer to soil, so removal of aboveground biomass after control would have greatly reduced total N inputs to soil in the 4-year removal duration. In addition, Grove et al. (2012) found evidence that allelopathic effects of Scotch broom were associated with application of fresh Scotch broom litter. In instances where Scotch broom biomass is retained on-site following control, it is plausible that legacy effects may persist for longer periods. We also note that differences in the initial harvest characteristics (e.g., amount of slash retained, soil disturbance, Table 1) among broom removal treatment areas may have influenced the response, limiting the inference of our results.

The effect of Scotch broom removal duration on the observed number of Scotch broom germinants is likely a result of past control efforts, bioassay species' effects on microclimate that inhibited germination, and a decrease in seed viability with time (Bossard and Rejmánek, 1994). For the 0- and 4-year duration treatments, Scotch broom was present and producing seed for longer periods that would have increased its seedbank relative to the 10-year and 14-year removals. Aggressive control of Scotch broom at the 10-year removal period was sufficient to create a 3- to 4-year gap in seed production, apparently resulting in a smaller seedbank. Our estimates of Scotch broom germination rates under the 0- and 4- year durations ranged from 83,000 to 578,500 germinants ha^{-1}. This estimate is realistic given Scotch broom's high seed production (Bossard and Rejmánek, 1994) and considering the density of plants at the site (730 plants ha^{-1}, Slesak et al. 2016) and the duration of time when seed was produced (up to 12 years). Williams (1981) estimated up to 550,000 germinants ha^{-1}, which is very similar to our estimates. These results indicate great potential for a negative soil legacy effect associated with the Scotch broom seedbank and demonstrate the need for aggressive and early control of Scotch broom to minimize the potential for reestablishment and reductions in long-term site productivity.

The effect of bioassay species on the number of Scotch broom germinants is likely associated with indirect differences in soil temperature

(Harrington, 2009) between Douglas-fir and both yarrow and Roemer's fescue, the latter of which had more rapid growth early in the bioassay with increased shading of the soil surface. Grasses have been shown to suppress Scotch broom seedling emergence, survival, and biomass (Harrington, 2011; Tran et al., 2018). Peter and Harrington (2018) found that retaining high amounts logging debris (i.e., bole only harvests used in the Long-Term Soil Productivity network, Powers et al., 2005) after forest harvesting resulted in an 88% reduction in fourth-year density of Scotch broom seedlings compared to lower retention, which was attributed to differences in microclimate between the logging debris levels. The decline in germinants associated with increased removal duration is likely a combined effect of a shorter period of seed production and accumulation due to past control treatments, reduced seedbank viability, and negative microclimate effects driven by Roemer's fescue and yarrow.

5. Conclusions

Our results indicate both positive and negative legacy effects of Scotch broom in glacial outwash soils of western Washington. In the case of Douglas-fir, there was no evidence of a nutrient-induced limitation to growth, providing indirect support for other mechanisms contributing to the response such as reduced EMF root colonization. In the case of yarrow and Roemer's fescue, there was clear evidence of a nutrient limitation to growth, indicating that the positive response in biomass in soils with the shortest Scotch broom removal duration was nutrient induced, likely from N. Legacy effects were relatively short-lived, likely because Scotch broom plant material was removed from the site following control. Scotch broom seedbank and germination can be dramatically reduced when efforts are made to control the species early after its establishment, including retention of logging debris following harvesting and the use of herbicides (Peter and Harrington 2018). Aggressive and early control of Scotch broom coupled with physical removal of any aboveground broom biomass from the site may be an effective means to minimize soil legacy effects on Douglas-fir growth and reduce the potential for Scotch broom re-establishment over time.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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