Plant Soil (2016) 398:281–289
DOI 10.1007/s11104-015-2662-7

REGULAR ARTICLE

Invasive scotch broom alters soil chemical properties in Douglas-fir forests of the Pacific Northwest, USA

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Received: 8 April 2015 / Accepted: 3 September 2015 / Published online: 14 September 2015

Abstract
Backgrounds and aims Scotch broom is an N-fixing invasive species that has high potential to alter soil properties. We compared soil from areas of Scotch broom invasion with nearby areas that had no evidence of invasion to assess the influence of broom on soil P fractions and other chemical properties.
Methods The study was conducted at two contrasting Douglas-fir sites in Oregon (OR) and Washington (WA), USA with broom invasion for 10 years. We used the Hedley sequential fractionation procedure to assess effects of Scotch broom invasion on P pools of varying bioavailability, and also measured total C, N and extractable nutrient cations.
Results Total soil C and N were significantly higher with broom present at the fine-textured OR site, but there was no effect at the coarse-textured WA site. There was no difference in labile-P measures between the presence and absence of Scotch broom at either site, but there were notable reductions (25–30 %) in the intermediately-available P fraction when broom was present. Extractable nutrient cations (notably K) were lower in the presence of broom at both sites, with the effects most pronounced at the fine-textured OR site.
Conclusions Lasting effects of Scotch broom invasion are likely to be associated with variable changes in soil C, N, and decreases in extractable nutrients and available P. These changes, and other documented effects of Scotch broom on soil, are likely to have lasting effects on Douglas-fir growth after Scotch broom removal that will vary depending soil nutrient status at a given site.

Keywords *Cytisus scoparius* · Hedley sequential fractionation · Forest soils · Invasive species effects on soils · Soil phosphorus

Responsible Editor: Hans Lambers.

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Introduction

Scotch broom (*Cytisus scoparius* (L.) Link) is a non-native, invasive plant species of major concern in coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) forests of the Pacific Northwest capable of ecosystem alteration and degradation. Ballistic dispersal, abundant production, and prolonged viability of its seeds enable Scotch broom to invade young forest, woodland, and prairie sites (Bossard 1993; Bossard and Rejmánek 1994; Smith 2000). Once established, Scotch broom has a competitive advantage over many

native plant species because of its rapid seedling growth rate (Grotkopp and Rejmánek 2007), and its ability to reduce availability of soil water and light (Watt et al. 2003; Wearne and Morgan 2004). Scotch broom is also a symbiotic nitrogen fixing species that can fix as much as 100 kg N ha^{-1} per year (Watt et al. 2003), which provides a competitive advantage in traditionally N-limited ecosystems (Vitousek and Horwath 1991).

Scotch broom invasion may alter soil properties and have lasting effects on soil functions even after its removal (Weidenhamer and Callaway 2010). At two nitrogen-deficient sites in Australia, Scotch broom was more competitive with native shrubs on Scotch broom-invaded soils than on native woodland soils, suggesting that the species altered soil chemical or other properties to favor its own regeneration and growth (Fogarty and Facelli 1999). Others have also documented reductions in plant growth using bioassay approaches (Haubensak and Parker 2004; Grove et al. 2012), but the mechanisms leading to these reductions are unclear. Introduction of alleopathic compounds by Scotch broom has been hypothesized as one possible mechanism, because species of the *Cytisus* genus are known to produce defensive alkaloid compounds that have been shown to detrimentally affect functions of some plants in controlled laboratory settings (Wink and Twardowski 1992). Grove et al. (2012) concluded that observed negative effects of Scotch broom on Douglas-fir growth were largely driven by reductions in ectomycorrhizal fungi (EMF) colonization, which would limit nutrient and water acquisition by the native trees.

Excess N inputs may also be a driver of altered soil properties as there is the potential to increase cation loss (Adams et al. 1997; Smethurst et al. 2001) and increase acquisition of soil P (Caldwell 2006; Shaben and Myers 2009). Increased P acquisition and availability associated with N-fixing species is supported theoretically (Houlton et al. 2008) and empirically (Giardina et al. 1995; Compton and Cole 1998), but the effect of increased acquisition on the availability of P pools over time is unclear. Phosphorus availability has large control over biological activity in general (Vitousek et al. 2010), and any change in soil pools following Scotch broom invasion could have lasting effects on soil functions. This would be especially true if readily-available pools of inorganic P are reduced (Caldwell 2006), accelerating the transformation of inorganic P into less-available organic and occluded forms (Walker and Syers 1976; Compton and Cole 1998). Shaben and Myers (2009) found no effect of Scotch broom on grass biomass when the two species were grown together in a bioassay study, but the investigators had amended the soils used in the bioassay with P fertilizer, ameliorating any potential Scotch broom-induced P deficiency if one existed. Although not conclusive, these studies support the notion that changes in soil P following Scotch broom invasion may lead to lasting effects on soil properties.

We assessed the effect of Scotch broom invasion for a period of 10 years on soil P fractions and other soil chemical properties at two sites with contrasting soils and invasion history. We hypothesized that the presence of Scotch broom would reduce readily available soil P pools and increase less-available pools, but have no effect on total P. We also hypothesized that Scotch broom would increase soil C and N and decrease nutrient cation pools. Our overall objective was to assess the potential for Scotch broom to have lasting effects on soil chemical properties.

Methods

Site descriptions

The assessment was conducted at two Douglas-fir sites affiliated with the North American Long-Term Soil Productivity (LTSP) study located in Washington (WA) and Oregon (OR) USA (Harrington and Schoenholtz 2010) (Table 1). Soils at the WA 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). Soils at the OR site are classified as fine-loamy, isotic, mesic Andic Dystrudepts formed in basic agglomerate residuum with slopes ranging from 2 to 40 % (Soil Survey Staff, USDA-NRCS). The regional climate is Mediterranean, characterized by cool, wet winters and warm, dry summers with periods of prolonged drought. Potential natural vegetation includes the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)/salal (*Gaultheria shallon* Pursh) plant association at the WA site (Henderson et al. 1989) and the western hemlock/Oregon-grape (*Mahonia nervosa* (Pursh) Nutt.)/swordfern (*Polystichum munitum* (Kaulf.) Presl) and western hemlock/Oregon grape-salal plant associations at the OR site (Halverson et al. 1986).

Table 1 Site characteristics and selected pre-treatment soil properties to a depth of 60 cm for study sites in Washington and Oregon (from Devine et al. 2011)

Characteristic or property	WA site	OR site
Location (latitude, longitude)	47.206 °N, 123.442 °W	45.196 °N, 122.285 °W
Elevation (m)	35	549
Mean annual temperature (°C)	10.7	11.2
Mean annual precipitation (cm)[1]	240	170
Soil particle size distribution (% sand/silt/clay)[2]	65 / 14 / 21	37 / 34 / 29
Bulk density (Mg m^{-3})	1.45 (0.05)[3]	0.98 (0.02)
Soil coarse fragments by mass (%)	67.6 (1.3)	37.7 (2.2)
Soil water holding capacity (mm)[4]	55	142
Total soil C (0–60 cm; Mg ha^{-1})	92.4 (5.8)	169.5 (12.0)
Total soil N (0–60 cm; Mg ha^{-1})	3.3 (0.15)	7.2 (0.41)

Precipitation was estimated for the period, 1950–2005 (PRISM Climate Group 2012)

[2] Determined with the hydrometer method

[3] Standard error in parentheses, $n=8$ for bulk density at OR site, $n=16$ for all others

[4] Estimated from water release curves constructed with pressure plate analyses on intact soil cores

Experimental Design

Each of the sites was clear cut harvested in spring 2003. Following cutting, Scotch broom began to proliferate across each of the sites from seed that was likely present in the seed bank prior to harvest (WA site) or brought in on the machinery during forest harvesting (OR site). In the fall of 2013, 3-m radius circular plots were replicated with Scotch broom either: i) present since harvest or ii) absent since harvest (likely never present). Replications were located in areas of each site where herbicide application was limited to a single site-preparation treatment and where logging debris was retained after harvesting (Harrington and Schoenholtz 2010). We were able to locate areas of Scotch broom presence or absence with high confidence due to the past work at these sites (Harrington et al. 2013). Because we could not randomly assign the presence or absence of Scotch broom to a given replication, we identified double the number of candidate replications for each level of Scotch broom and then randomly selected half for inclusion in this study. This approach allowed for unbiased estimation of soil conditions within each of the Scotch broom conditions. Plots with broom present were assigned to areas where broom abundance was greatest near plot center, while plots with broom absent were assigned to areas between rows of planted Douglas-fir and were not under the canopy.

Soil samples were collected in the fall of 2013 at both sites using bucket augers. At each treatment replication, three samples were randomly selected from a nine point grid that encompassed the central 2-×2 m area of the plot. Given the plot arrangement described above, this sampling scheme resulted in samples being collected from areas that were either in close proximity to broom (in broom-present plots) or in areas with limited overstory cover (in broom-absent plots). Samples were collected at 0–15 and 15–30 cm depth increments, which generally comprised the A horizon of each soil type. The O horizon was discontinuous and shallow when present; we removed any O horizon prior to sampling to focus exclusively on differences in mineral soil properties between broom presence and absence. Samples were composited in a bucket, thoroughly mixed, and a subsample was placed in a Ziploc bag for transport. We also measured Scotch broom basal area (at 15 cm height), stem density, average height, and crown cover within each treatment replication.

Analysis

Soil samples were returned to the laboratory, air-dried, and sieved to pass a 2 mm mesh. Total soil C and N were measured on a 1-g subsample that was ground with a mortar and pestle to pass a 0.25 mm mesh, followed by dry combustion using a LECO Dumas combustion

technique on a Fisons NA1500 NCS Elemental Analyzer (ThermoQuest Italia, Milan, Italy). The Mehlich method was used to extract soil P, Ca, Mg, and K, and extract concentrations were measured with inductively coupled plasma spectroscopy (Varian Vista MPX, Varian, Palo Alto, CA, USA). We used a modified Hedley sequential fractionation procedure (Hedley et al. 1982) to separate soil P into five fractions of varying availability as described in Cross and Schlesinger (1995) (Table 2). Extracts and digests from each P fraction were analyzed for P concentration with inductively coupled plasma spectroscopy.

Differences in soil chemical parameters between areas with Scotch broom present or absent were assessed using *t*-tests. Equality of variance between the two populations was calculated and the approximation of Cochran and Cox (1950) was used to assess significance when the variance was unequal. We used an alpha level of 0.10 for significance and conducted all statistical analyses in SAS V9.4 (SAS Institute 2013).

Results

Scotch broom characteristics

Scotch broom invasion and occurrence was much higher at the WA site where it formed dense thickets, compared to lower prevalence at the OR site where it occurred in dispersed patches (R. Slesak, pers. obs.). Despite this, Scotch broom density in the 3 m radius plots was similar, being 0.22 (±0.13) and 0.21 (±0.13) stems m^{-2} at the WA and OR sites, respectively. However, all other measures of Scotch broom abundance were greater at the OR site compared to the WA site as follows: 2.22 (±1.07) vs. 1.37 (±0.86) cm^2 m^{-2} for basal area, 272 (±38) vs. 176 (±23) cm for average height, and 76.5 (±17.2) vs. 61.3 (±17.5) percent for crown cover, at the OR and WA sites, respectively. Differences in broom abundance are likely due to higher soil quality at the OR site compared to the WA site (Table 1).

Differences in soil C, N, and extractable cations

There was no difference in total soil C and N when Scotch broom was present or absent at the WA site, but C and N in the 0–15 cm depth increment were significantly greater when Scotch broom was present at the OR site (Table 3). The estimated difference between the presence and absence of Scotch broom at that site and depth was 2.59 (90 % CL: 0.75, 4.44) and 0.07 (90 % CL: 0.01, 0.13) percent for C and N, respectively. At the WA site, C:N at 0–15 cm depth was significantly lower (−2.6; 90 % CL: −4.6, −0.8) when Scotch broom was present, but significantly higher (2.3; 90 % CL: 0.2, 4.4) when Scotch broom was present at the OR site. Similar differences in C:N were observed at the 15–30 cm depth increment at the OR site, but not the WA site (Table 3) .

Extractable K in the 0–15 cm depth increment was lower when Scotch broom was present at both sites, and also in the 15–30 cm increment at the WA site. There was no difference in extractable Ca and Mg at 0–15 cm depth between the presence and absence of Scotch broom at either site, but both nutrients were significantly lower when Scotch broom was present at the OR site at 15–30 cm depth.

Differences in soil P fractions

There was no difference in Mehlich extractable soil P when Scotch broom was present or absent at either site

Table 2 Extracting solution and description of each P-fraction used in the Hedley sequential fractionation method (adapted with permission from DeBruler 2014)

P fraction	Extractant	Description
Labile P	0.5 M $NaHCO_3$ (Bicarb)	Hydrolysable inorganic and organic P
Moderately labile P	0.1 M NaOH (NaOH)	Fe- and Al-associated phosphates and organic P
Moderately recalcitrant P	0.1 M NaOH with sonication (Sonic)	P on internal surfaces of soil aggregates and chemisorbed to soil surfaces
Recalcitrant P	M HCI (HCl)	Ca-bound inorganic P
Occluded P	Sulfuric acid digestion (Residual)	Non-extractable and very slow turnover P
Total	None	Sum of all fractions

Table 3 Soil chemical properties when Scotch broom was present or absent for a period of 10 years at two sites (asterisks indicate significant differences within a site, α=0.10)

Soil chemical property	Washington site		Oregon site	
	Scotch broom			
	Present	Absent	Present	Absent
0–15 cm depth				
C (%)	5.94 (0.27)	5.90 (0.26)	9.88 (0.91)*	7.29 (0.60)
N (%)	0.24 (0.01)	0.22 (0.01)	0.42 (0.02)*	0.35 (0.03)
C:N	24.4 (0.6)*	27.0 (0.9)	23.0 (1.1)*	20.7 (0.6)
P (mg kg^{-1})[1]	15.3 (2.1)	18.7 (1.8)	4.8 (0.3)	4.1 (0.4)
Ca (mg kg^{-1})	280 (65)	253 (26)	1165 (73)	1357 (145)
Mg (mg kg^{-1})	28 (5)	35 (3)	164 (14)	237 (43)
K (mg kg^{-1})	39 (3)*	63 (11)	286(28)*	341(18)
15–30 cm depth				
C (%)	4.00 (0.23)	4.00 (0.31)	6.51 (0.40)	5.48 (0.56)
N (%)	0.16 (0.01)	0.15 (0.01)	0.30 (0.02)	0.27 (0.03)
C:N	24.9 (0.7)	27.0 (1.1)	21.9 (0.6)*	20.2 (0.5)
P (mg kg^{-1})	9.1 (0.8)	11.3 (1.7)	2.9 (0.1)	2.9 (0.3)
Ca (mg kg^{-1})	113 (20)	96 (13)	707 (70)*	1168 (166)
Mg (mg kg^{-1})	11 (1)	14 (2)	106 (14)*	225 (54)
K (mg kg^{-1})	25 (1)*	31 (2)	201 (22)	255 (21)

Standard error in parenthesis (at each site, n=20 for Scotch broom present, n=10 for Scotch broom absent)

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

and at both depths (Table 3). For the Hedley fractions, there was a significant difference in the moderately labile NaOH fraction between the presence and absence of Scotch broom (Fig. 1). At the WA site, NaOH-P was 234 mg kg^{-1} lower (~30 %) when Scotch broom was present at 0–15 cm depth (Fig. 1), and 160 mg kg^{-1} lower (~25 %) at the 15–30 cm depth (data not shown). A similar non-significant difference (p=0.15) was observed at the OR site at 0–15 cm depth (Fig. 1), but not 15–30 cm (data not shown). There were no significant differences in other P fractions between the presence and absence of Scotch broom at either site or depth increment.

Discussion

Soil C and N

Given its ability to fix moderate quantities of N (Watt et al. 2003), we hypothesized that soil N would be higher when Scotch broom was present compared to absent and that soil C would be greater when Scotch broom was present as well given the fundamental linkage between soil C and N pools (Binkley 2005). The contrasting findings we observed at the two sites indicate that soil C and N changes are dependent on site characteristics, which was also observed by Grove et al. (2012). On a relatively rich loamy soil in northern California, Caldwell (2006) found that soil C and N at 0–5 cm were higher when Scotch broom was present, with no effect on C:N. Other studies have reported numerically greater total soil C and N when Scotch broom was present (Wheeler et al. 1987; Fogarty and Facelli 1999; Shaben and Myers 2009). At a location near our WA site, Haubensak and Parker (2004) observed small changes in soil C and N along a Scotch broom density gradient even though density of the shrub at their site was an order of magnitude greater than at our sites. One possible factor contributing to the variable response is differences in soil texture between sites, as our OR site had a finer texture similar to the site assessed by Caldwell (2006), and soils at our WA were coarse-textured and very similar to those at the site assessed by

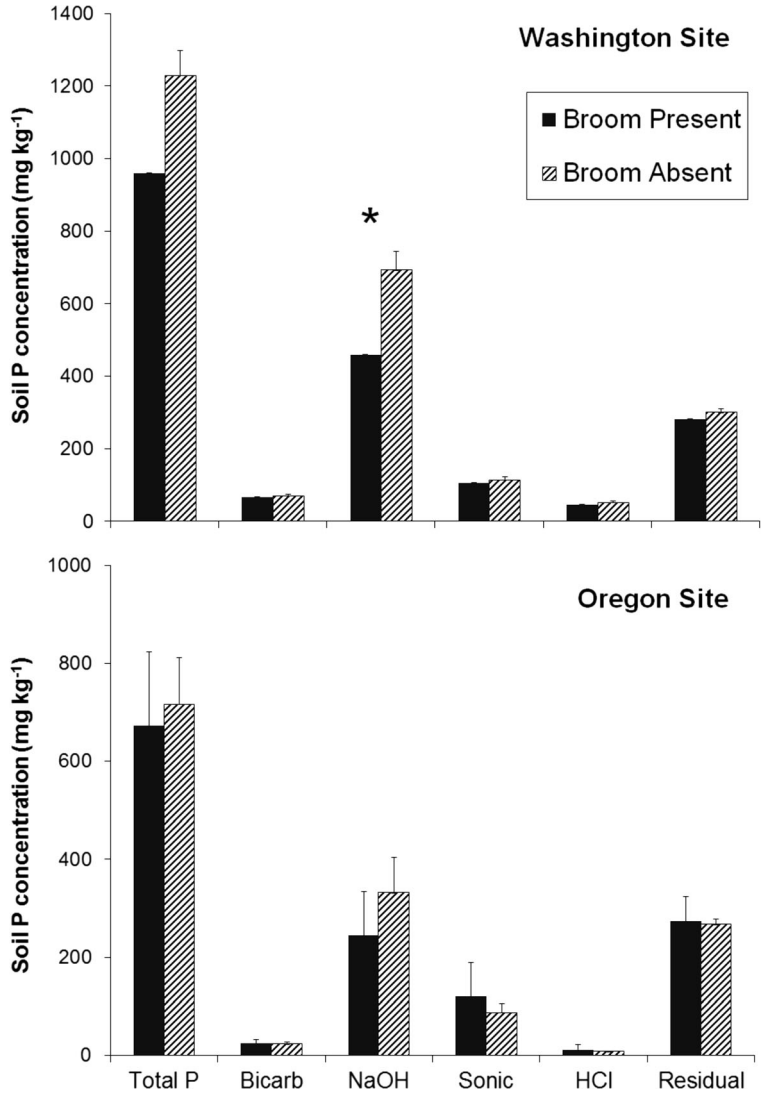

Fig. 1 Soil P concentrations from sequential P fraction technique by site in the presence or absence of Scotch broom (asterisks indicate significant differences within a fraction and site). Error bars are the standard error of the mean. See Table 2 for descriptions of the P fractions

Haubensak and Parker (2004). Coarser soils are generally more susceptible to leaching, so N inputs from Scotch broom may have leached deeper into the soil profile and were not incorporated into soil pools at 0–30 cm depth. The contrasting response could also be due to differences in broom abundance and form between sites (e.g., extent of canopy cover; Blaser et al. (2013)).

Extractable soil Ca, Mg, and K

Increased N inputs when Scotch broom is present have the potential to reduce soil nutrient pools via displacement on the exchange complex and increased mobility which can lead to leaching and a reduction in soil cation pools (Van Miegroet and Cole 1984). The lower extractable K we observed at both sites when Scotch broom was present is likely caused by this mechanism, as K is more easily displaced from the exchange complex compared to other nutrient cations (Brady and Weil 2008) and susceptible to leaching when 2:1 clay content is low. The lower extractable Ca and Mg at the OR site when Scotch broom was present could also be a result of this mechanism, or possibly due to greater uptake of Ca and Mg given the greater basal area, height, and crown cover of Scotch broom at the OR site. Scotch broom does not appear to have higher nutrient requirements than other common shrub species (Lambert et al. 1989), but its high growth rate in general would increase overall Ca and Mg uptake compared to other vegetation. However, correlation analysis indicated there was no

relationship between Scotch broom abundance and extractable soil nutrients (data not shown), so this possibility seems less likely than leaching.

Soil P fractions

Comparison of our soil P findings with other studies is difficult as we are unaware of any that have assessed differences in P fractions following Scotch broom invasion using the sequential fractionation technique. A number of studies have demonstrated that the presence of N-fixing vegetation can influence soil P pools and cycling including the presence of red alder (*Alnus rubra* Bong.) in forested ecosystems (Compton and Cole 1998; Giardina et al. 1995) and Scotch broom in grassland ecosystems (Caldwell 2006; Shaben and Myers 2009). The effect is generally attributed to greater P demand coupled with increased P acquisition associated with higher phosphatase concentrations that occur with higher N inputs (Vitousek et al. 2010; Giardina et al. 1995). Caldwell (2006) observed lower inorganic phosphorus under Scotch broom compared to nearby prairie, but there was no difference in the organic P pool even though phosphatase was significantly higher in the presence of Scotch broom. Here, we observed lower NaOH-P when Scotch broom was present, but there was no discernable effect on the most labile Bicarb-P fraction or other, more recalcitrant fractions. The NaOH-P fraction extracts organic and inorganic P sorbed to Fe and Al hydroxides, and has historically been thought to have intermediate availability for biologic uptake (Cross and Schlesinger 1995). Although we do not know for certain the mechanism(s) leading to lower NaOH-P in the presence of Scotch broom, it seems likely that Scotch broom uptake contributed to the reduction as there was little evidence of transformation and incorporation into other soil P pools (Fig. 1).

Implications

The contrasting effect of Scotch broom on soil C, N, Ca, and Mg between sites indicates that any effects on soil functions associated with these elements will likely be dependent on soil-site conditions, similar to the conclusion of Ehrenfeld (2003) as related to invasive species in general. Shaben and Myers (2009) demonstrated that Scotch broom invasion can dramatically change native plant species composition through displacement of native species and the creation of conditions that allow for increased abundance of non-native species, including altered soil chemistry. Given the fundamental role that soil C (and by extension, soil OM) plays in nutrient cycling and soil productivity in general (e.g., Powers et al. 1990), changes in aboveground productivity and vegetative composition are likely to persist following Scotch broom removal (Weidenhamer and Callaway 2010) with the effects being most pronounced at sites with greatest relative change in soil pools of C and nutrients.

Even with consistent effects of broom, such as the decrease in K at both sites when broom was present, the relative effect on Douglas-fir growth is likely to vary. Foliar analysis of Douglas-fir at these sites (T. Harrington, unpublished data) indicates moderate to severe deficiency in N and K (1.3 and 0.6 % respectively; Ballard and Carter 1986) at the WA site, but sufficiency for all major nutrients at the OR site. In the case of K, low initial soil pools at the WA site coupled with reductions in the presence of broom may lead to further constraints on Douglas-fir nutrition in the future, even if N availability was increased (Mika and Moore 1990). In contrast, initial nutrient pools at the OR site appear to be sufficient to maintain growth even with the larger absolute reductions in soil K and other extractable cations when broom was present. In fact, the increase in soil N with broom present at the OR site has the potential to increase stand growth following crown closure and broom dieback given the pivotal role this element plays in stand productivity across a range of nitrogen availability (Devine et al. 2011).

The long-term effect of the reduced soil NaOH-P we observed when Scotch broom was present is unclear because our understanding of the bioavailability of Hedley P fractions is still evolving (Condron and Newman 2011). Chen et al. (2003) showed that the NaOH-P fraction is one of the primary pools available for plant uptake in a variety of grassland soils, and Richter et al. (2006) demonstrated the importance of this pool to long-term P bioavailability in an aggrading pine forest. At our sites, the NaOH-P also comprised a majority of total P (Fig. 1), but we only sampled to 30 cm depth and some studies have shown P uptake by trees from deeper portions of the soil profile to be large (Sitters et al. 2013). If a P availability effect of Scotch broom on vegetation growth occurs (Vitousek et al. 2010), it would manifest later in stand development as there is no current evidence of P limitation to Douglas-fir growth (T. Harrington, unpublished data).

Grove et al. (2012) observed decreases in Douglas-fir growth following Scotch broom invasion at a nearby site which they largely attributed to lower ectomycorrhizal fungi (EMF) colonization of Douglas-fir roots when Scotch broom was present. Effects on Douglas-fir growth following Scotch broom removal may be exacerbated by a concurrent reduction in EMF and nutrient pools which in combination would greatly reduce nutrient uptake needed for growth. Such an effect would be much larger when initial soil nutrient pools are low such as at the WA site, underlying a need to consider site-specific factors when evaluating strategies for restoration following broom removal.

Conclusions

Based on our findings, we conclude that Scotch broom is likely to have lasting effects on soil functions because of its influence on soil chemical properties after being present for 10 years. Increases in soil C and N, alteration of C:N, and decreases in soil extractable nutrients and the NaOH-P fraction that we observed agree with the limited findings from previous studies and conceptual theory. Further work is needed to clearly identify the relative importance of these changes to soil functions and vegetative response to develop site-specific strategies for ecosystem restoration after Scotch broom removal.

Acknowledgments This work was funded by the USDA Agriculture and Food Research Initiative-Controlling Weedy and Invasive Plants program, the USDA Forest Service-Pacific Northwest Research Station, and the University of Minnesota. We are grateful to Randall Greggs of Green Diamond Resource Company and Mike Warjone of Port Blakely Tree Farms LLC for logistical support and access to the study sites. Special thanks are given to James Dollins and Dave Peter for assisting with field sampling and study establishment, and to Stephen Schoenholtz and Daniel DeBruler for conducting the laboratory analyses.

References

Adams MB, Angradi TT, Kochenderfer IN (1997) Stream water and soil solution responses to 5 years of nitrogen and sulfur additions at the fernow experimental forest, West Virginia. For Ecol Manag 95:79–91

Ballard TM and Carter RE (1986) Evaluating forest stand nutrient status. Land management report No. 20. British Columbia Ministry of Forests, Victoria, Canada

Binkley D (2005) How nitrogen fixing trees change soil carbon. In: Binkley D, Menyailo O (eds) Tree species effects on soils: implications for global change, NATO science series. Kluwer Academic Publishers, Dordrecht

Blaser WJ, Sitters J, Hart SP, Edwards PJ, Venterlink HO (2013) Facilitative or competitive effects of woody plants on understorey vegetation depend on N-fixation, canopy shape, and rainfall. J Ecol 101:1598–1603

Bossard CC (1993) Seed germination in the exotic shrub cytisus scoparius (scotch broom) in California. Madrono 40:47–61

Bossard CC, Rejmánek M (1994) Herbivory, growth, seed production, and resprouting of an exotic invasive shrub, Cytisus scoparius. Biol Conserv 67:193–200

Brady NC, Weil RR (2008) Chapter 9: the colloidal fraction. In: Brady NC, Weil RR (eds) The nature and properties of soils, 14th edn. Pearson-Prentice Hall, Upper Saddle River, NJ

Caldwell BA (2006) Effects of invasive scotch broom on soil properties in a pacific coastal prairie soil. Appl Soil Ecol 32:149–152

Chen CR, Sinaj S, Condron LM, Frossard E, Sherlock RR, Davis MR (2003) Characterization of phosphorus availability in selected New Zealand grassland soils. Nutr Cycl Agroecosyst 65:89–100

Cochran WG, Cox GM (1950) Experimental designs. John Wiley and Sons, New York, NY, 454 pp

Compton JE, Cole DW (1998) Phosphorus cycling and soil P fractions in Douglas-fir and red alder stands. For Ecol Manag 110:101–112

Condron LM, Newman S (2011) Revisiting the fundamentals of phosphorus fractionation of sediments and soils. J Soils Sediments 11:830–840

Cross AF, Schlesinger WH (1995) A literature review and evaluation of the Hedley fractionation: applications to the biogeochemical cycle of soil phosphorus in natural ecosystems. Geoderma 64:197–214

DeBruler DG (2014) Soil carbon, nutrients, and phosphorus fractions: responses to weed control and harvest residual retention in two 10-year-old Douglas-fir (*Pseudotsuga menziesii)* stands of the Pacific Northwest. M.Sc. Thesis. Virginia Polytechnic Institute and State University, Blacksburg, Virginia

Devine WD, Harrington TB, Terry TA, Harrison RB, Slesak RA, Peter DH, Harrington CA, Shilling CJ, Schoenholtz SH (2011) Five-year vegetation control effects on aboveground biomass and nitrogen content and allocation in Douglas-fir plantations on three contrasting sites. For Ecol Manag 262: 2187–2198

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503–523

Fogarty G, Facelli JM (1999) Growth and competition of cytisus scoparius, an invasive shrub, and Australian native shrubs. Plant Ecol 144:27–35

Giardina CP, Huffman S, Binkley D, Caldwell B (1995) Alders increase soil phosphorus availability in a Douglas-fir plantation. Can J For Res 25:1652–1657

Grotkopp E, Rejmánek M (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. Amer J Bot 94(4):526–532

Grove S, Haubensak KA, Parker IM (2012) Direct and indirect effects of allelopathy in the soil legacy of an exotic plant invasion. Plant Ecol 213:1869–1882

Halverson NM, Topik C and Van Vickle R (1986) Plant association and management guide for the western hemlock zone. Mount hood national forest. USDA forest service, Pacific Northwest Region, Portland, OR. R6-ECOL-232A-1986. pp. 62–65

Harrington TB, Schoenholtz SH (2010) Effects of logging debris treatments on 5 years development of competing vegetation and planted Douglas-fir. Can J For Res 40:500–510

Harrington TB, Slesak RA, Schoenholtz SH (2013) Variation in logging debris cover influences competitor abundance, resource availability, and early growth of planted Douglas-fir. For Ecol Manag 296:41–52

Haubensak KA, Parker IM (2004) Soil changes accompanying invasion of the exotic shrub cytisus scoparius in glacial outwash prairies of western Washington [USA]. Plant Ecol 175:71–79

Hedley MJ, Stewart JWB, Chauhan B (1982) Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. Soil Sci Soc Am J 46(5):970–976

Henderson JA, Peter DH, Lesher RD and Shaw DC (1989) Forested plant associations of the Olympic national forest. USDA Forest Service Report No. R6-ECOL-TP 001–88. pp. 350–353

Houlton BZ, Wang Y, Vitousek PM, Field CB (2008) A unifying framework for dinitrogen fixation in the terrestrial biosphere. Nature 454:327–330

Powers RF, Alban DH, Miller RE, Tiarks AE, Wells CG, Avers PE, Cline RG, Fitzgerald RO, Loftus NS Jr. (1990) Sustaining site productivity in North American forests: problems and prospects. In: Gessel SP et al. (eds) In Sustained productivity of forest soils. Forestry Publications, University of British Columbia, Vancouver, p. 49–80

PRISM Climate Group (2012) PRISM (Parameter-elevation Regressions on Independent Slopes Model) climate mapping system. Oregon State University. http://prism.oregonstate.edu

SAS Institute Inc (2013) The SAS system for windows, version 9.4. Cary, North Carolina

Lambert MG, Jung GA, Harpster HW, Lee J (1989) Forage shrubs in north island hill country 4. Chemical composition and conclusions. N Z J Agric Res 32:499–506

Mika PG, Moore JA (1990) Foliar potassium status explains Douglas-fir response to nitrogen fertilization in the inland northwest, USA. Water Air Soil Pollut 54:477–491

Richter DD, Allen HL, Li J, Markewitz D, Raikes J (2006) Bioavailability of slowly cycling soil phosphorus: major restructuring of soil P fractions over four decades in an aggrading forest. Ecosyst Ecol. doi:10.1007/s00442-006-0510-4

Shaben J, Myers JH (2009) Relationships between scotch broom (cytisus scoparius), soil nutrients, and plant diversity in the Garry oak savannah ecosystem. Plant Ecol. doi:10.1007/s11258-009-9655-7

Sitters J, Edwards PJ, Venterink HO (2013) Increases of soil C, N, and P pools along an acacia tree density gradient and their effects on trees and grasses. Ecosystems 16:347–357

Smethurst PJ, Herbert AM, Ballard LM (2001) Fertilization effects on soil solution chemistry in three eucalypt plantations. Soil Sci Soc Am J 65:795–804

Smith JMB (2000) An introduction to the biogeography and ecology of broom (cytisus scoparius) in Australia. p. 140–144 in Sheppard AW and Hosking JR, broom management, process of a workshop, ellerston and moonan, Australia, Nov. 16–17, 1998. Plant Prot Q 15(4):134–186

Van Miegroet H, Cole DW (1984) The impact of nitrification on soil acidification and cation leaching in a red alder ecosystem. J Environ Qual 13:586–590

Vitousek PM, Horwath RW (1991) Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13(2):87–115

Vitousek PM, Porder S, Houlton B, Chadwick O (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. Ecol Appl 20:5–15

Walker TW, Syers JK (1976) The fate of phosphorus during pedogenesis. Geoderma 15:1–19

Watt MS, Whitehead D, Mason EG, Richardson B, Kimberly MO (2003) The influence of weed competition for light and water on growth and dry matter partitioning of young Pinus radiata, at a dryland site. For Ecol Manag 183:363–376

Wearne LJ, Morgan JW (2004) Community-level changes in Australian subalpine vegetation following invasion by the non-native shrub cytisus scoparius. J Veg Sci 15:595–604

Weidenhamer JD, Callaway RM (2010) Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. J Chem Ecol 36:59–69

Wheeler CT, Helgerson OT, Perry DA, Gordon JC (1987) Nitrogen fixation and biomass accumulation in plant communities dominated by cytisus scoparius L. in Oregon and Scotland. J Appl Ecol 24:231–237

Wink M, Twardowski T (1992) Allelochemical properties of alkaloids: effects on plants, bacteria and protein biosynthesis. In: Rizvi SJH, Rizvi V (eds) Allelopathy: basic and applied aspects. Chapman and Hall, New York, USA