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Effects of Nitrogen-Fixing Shrubs in Washington and Coastal California[1]

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Abstract: Open grasslands in California and Washington are being invaded by two closely related European shrubs, French broom and Scotch broom, that are considered among the most invasive and damaging of wildland species in those habitats. In this study, we present evidence of their effects on soil nitrogen (N) and the implications for restoration. Using natural abundance ^{15}N signatures of leaves, we show that N fixation by brooms varies across sites and may depend on a suite of site-specific factors. Nonetheless, in sites in both California and Washington, we observe up to a twofold increase in soil N availability, as assayed in the laboratory. Across a range of sites, we determined that burning decreases total soil N by nearly 40%. We found burning to have the simultaneous effect of decreasing the broom seedbank by 68% after one burn. In a separate experiment, we removed broom and added sawdust to the soil to test whether a N-immobilization effect would help slower growing native perennial grasses in competition with European annual grasses. We found that although sawdust effectively decreased N availability after a 2-yr application period, we could not effectively target which group of species would benefit most.
Nomenclature: French broom, *Genista monspessulana* L. Link; Scotch broom, *Cytisus scoparius* L. Link.
Additional index words: Grassland, nitrogen fixation, restoration, shrub.

INTRODUCTION

Open grasslands on the west coast of North America are being invaded by two closely related European shrubs, French broom and Scotch broom, that are considered among the most invasive and damaging of wildland species in California (Bossard 2000). The invasion of these shrubs is associated with a reduction in native plant diversity (Parker and Kersnar 1989), insect populations (Bossard 2000), and increased fuel loads (Bossard 2000). A number of factors most likely contribute to the encroachment of these shrubs into grasslands, including fire exclusion and cessation of grazing. However, because these brooms are members of the legume family, they have the ability to fix nitrogen (N), which may affect both their success at invasion and their long-term effects. In this study, we present evidence that broom invasion is associated with changes in soil N dynamics and the implications for restoration. Specifically, we discuss evidence for N fixation and changes in soil N availability and the total N pool in surface soils associated with broom invasion. We also present results of a restoration experiment, where we manipulated soil N after broom removal and assessed the effect of that manipulation on competition between exotic annual and native perennial grasses.

MATERIALS AND METHODS

Study Sites. In California, our sites were located within national, state, and city park boundaries in San Mateo and Marin counties, nearby San Francisco. In Washington, our sites were located in Johnson Prairie on the Fort Lewis Military Reservation, approximately 80 km south of Seattle in the Puget Sound trough. The climate at the California sites is typical Mediterranean, with the growing season beginning with autumn germinating rains and continuing until the termination of the rainfall period, typically anywhere from late April to early June. Temperatures during the annual summer drought are modified by coastal fog. In the Washington site, the climate is characterized by mild temperatures with narrow daily fluctuations (6 to 10 C). The winters are wet and mild,

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summers relatively dry and cool. None of the California sites have active livestock grazing or prescribed fire regimes; the Washington site was burned approximately 15 yr before our study. In California, Mediterranean annual grasses codominate these herbaceous communities with native perennial grasses and forbs. All our California sites have substantial French broom invasion occurring into the otherwise intact open grassland. At more than half of those sites, Scotch broom is also invading; the proportion of French to Scotch broom is approximately 10:1. In Washington, stands of Scotch broom are replacing a grassland community dominated by Idaho fescue [*Festuca idahoensis* Elmer (Poaceae)] and small herbaceous perennials such as camas [*Cammassia quamash* (Pursh) E. Greene (Liliaceae)] and Curtis' aster [*Aster curtisii* Torr. and Gray (Asteraceae)]. At the time of writing this article, French broom does not occur in these prairies.

Evidence for N Fixation. In spring 1998, we collected soil and plant material from eight coastal prairie sites in California. In brief, we collected leaf tissue from Scotch broom, French broom, and one native, non–nitrogen-fixing shrub, *Baccharis pilularis* ssp. *consanguinea* (DC) C.B. Wolf (hereafter "coyote bush"). Soil material was collected at each site simultaneously. All soil and plant material was prepared following standard protocol and then analyzed on a mass spectrometer for ^{15}N natural abundance signature (see Haubensak 2001 for detail).

Total Soil N Pool. In December 1996, we randomly chose 18 Scotch broom stands that were at least 20 m in diameter in Johnson Prairie, Washington. We identified the stand edge, where broom density was between 1 and 2 individuals per square meter. From the stand edge, transects were run in opposing directions—9 m toward the center of the infestation and 9 m into adjacent uninvaded grassland. At 3-m intervals, we sampled surface soils (excluding the litter) to a depth of 10 cm with a coring device of 5 cm diameter. We simultaneously measured Scotch broom aboveground biomass at each soil sampling interval as a possible predictor of total soil N. Soils were prepared according to standard protocol for total N analysis (See Haubensak and Parker, 2004, for detail). Total soil carbon (C) values were measured at the same time.

Soil N Availability (Laboratory Incubation). We sampled soils for N availability in April 1997 at the Washington site, and in March 2000 at the California site. In both sites, we collected surface soils inside Scotch broom and French broom stands and outside the stands in uninvaded grassland (n = 12 patches in Washington; n = 10 patches in California). Soil cores were taken from the top 10 cm of soil after litter material was removed, in areas at least 3 m inside the edge of a broom stand. Outside of and adjacent to each patch, a core was taken from uninvaded grassland soil after similar removal of organic material from the soil surface. Cores were placed in coolers and brought back to the laboratory at University of California–Berkeley for immediate analysis in a 7-d laboratory aerobic incubation. The procedure for the soil analysis follows "Potassium chloride extracts."[3]

Soil N Availability (Greenhouse Bioassay). We grew yarrow (*Achillea millefolium*), a common herbaceous species, in Washington soils from inside and outside of Scotch broom patches (hereafter "broom soil" and "grass soil," respectively). The soils used were the same as those collected for the laboratory incubation described above. See Haubensak and Parker (2004) for detail on greenhouse conditions, harvesting methods, and analysis.

Effects of Burning on Total Soil N Pool and Broom Seedbank. We collected soils (top 10 cm) from 26 areas in Marin County, California, that had previously been occupied by broom (>90% cover) and that had been burned from one to four times. We also sampled in six areas that were broom invaded and had not been burned, as unburned controls. Soils were analyzed for %N (as described in Haubensak and Parker, 2004). We germinated separate soil samples in a lathehouse and then sieved the soil to count seeds that had not germinated. We therefore included germinable, viable, and dead seeds in our analysis. Dead seeds only made up an average of 2% of all seeds.

Use of Sawdust to Immobilize N and Benefit Native Species in Competition with Annual Grasses. In December 1998, we cut down a large stand of mature French and Scotch broom, then implemented an experiment to test the effectiveness of sawdust addition on soil N immobilization in plots where we planted perennial (native) and annual (exotic) grasses. The aim was to decrease the performance of rapidly colonizing and fast-growing exotic annuals so that native grass persistence and establishment would be facilitated. See Haubensak (2001) for details regarding plot set-up, species combinations, and rates and amounts of sawdust addition. At the end of the 1999 and 2000 growing seasons,

[3] "Potassium chloride extracts," http://www.stanford.edu/group/Vitousek/.

aboveground biomass of both annual and perennial grasses was harvested, dried, and weighed. During both growing seasons, soil N availability was monitored in 7-d laboratory incubations (see Soil Available N, Laboratory Incubation, above).

RESULTS

Leaf ^{15}N Signatures and Evidence for Fixation. In our foliar survey of evidence for N fixation, leaf tissue of both brooms tended to have a narrower range of ^{15}N values around zero (the signal of the atmosphere) (~2.5‰) compared with that of the reference non–N-fixer, coyote bush, which spanned a wider range around zero (~3.7‰). Averaged across sites, French broom had leaf ^{15}N signatures closer to the atmospheric signal compared with Scotch broom (~0.48‰ for French broom and ~1.0‰ for Scotch broom). At five of the eight sites, the ^{15}N signature of the leaves of French broom was remarkably clustered around zero (from −0.29 ± 0.12‰ to 0.25 ± 0.47‰). In addition, both brooms had higher concentrations of N in their leaves, on average, compared with the non–N-fixing coyote bush (~3.8, 4.5, and 2.8% for French, Scotch, and coyote bush, respectively).

Total Soil N Pool. In Washington, the total N pool of the surface soil increased from 427.06 g/m^2 in the uninvaded grassland to 454.67 g/m^2 inside dense Scotch broom patches, an increase of about 6%. This increase was statistically significant, but aboveground biomass explained little variance (R^2 = 0.07; P = 0.003; N = 126). Total C pool increased slightly (~2%) across the gradient. The total C pool simultaneously increased from grassland into Scotch broom patches, although slightly less than N, resulting in a small decrease in the C to N ratio from uninvaded to Scotch broom–invaded soils (R^2 = 0.190; P < 0.0005; N = 125).

Soil N Availability (Laboratory Incubation and Greenhouse Bioassay). The two assays that we used to assess soil N availability provided conflicting results. In the laboratory incubation, broom soils had 2 to 3 times more N availability than the grass soils, in both California and Washington (P < 0.05). In the greenhouse, however, our bioassay species, yarrow, grew poorer in the broom soil compared with the grass soil (the assay was conducted on Washington soils only). Plants were 30% smaller aboveground in the broom soil and had 32% less root biomass compared with those grown in the grass soil (P < 0.05 for both shoots and roots).

Effects of Burning on Soil N and Broom Seedbank. We found that total N in the top 10 cm of mineral soil

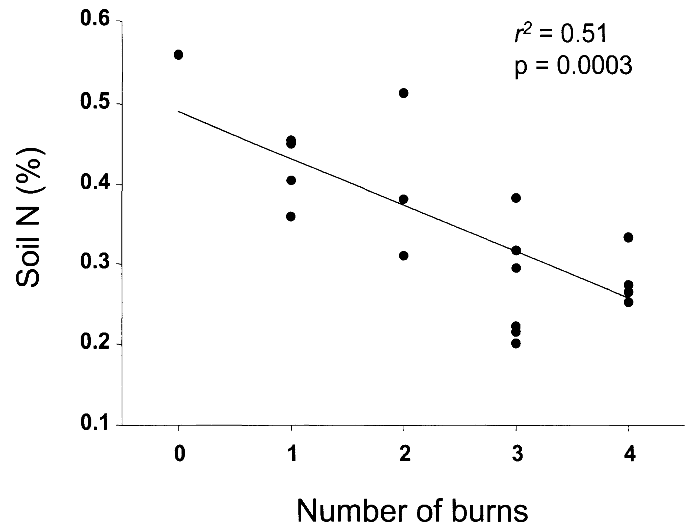

Figure 1. Total nitrogen (N) in surface (top 10 cm) soil sampled in a range of broom-invaded sites in Marin County, California, that had been burned from zero (control) up to four times. Each point represents the mean value at one site, in which 10 samples were collected randomly.

decreased as the number of burns at a site increased from ~0.5% at the unburned control sites to 0.3% at sites that had been repeatedly burned (four times) (Figure 1). Simultaneously, we found that the initial flush of broom germination after one prescribed fire removed an average of 68% of the seedbank. We also found, however, that repeated burns in the same site did not significantly reduce the seedbank any further (P > 0.05). See Alexander and D'Antonio (2003) for further detail.

Use of Sawdust to Immobilize N and Benefit Native Species in Competition with Annual Grasses. Soil N availability was unaffected by sawdust addition until the end of the second year of application; at that point, there was a significant decrease in perennials-only plots (P < 0.05). By the end of the 2-yr experiment, two of the three native species suffered 100% mortality in the perennials-plus-annuals plots. Therefore, we were only able to assess the effect of annual grass competition, and how that effect was mitigated by sawdust, on red fescue (*Festuca rubra*) alone. We found that in the presence of competition with annual grasses, there was no mitigating effect of sawdust addition on red fescue growth (Figure 2). In plots where perennial grasses grew alone (without annuals), red fescue growth was strongly negatively affected by sawdust addition.

DISCUSSION

Our results show that these broom species can alter soil N dynamics and that restoration efforts can affect, or be affected by, those alterations. Our work also sug-

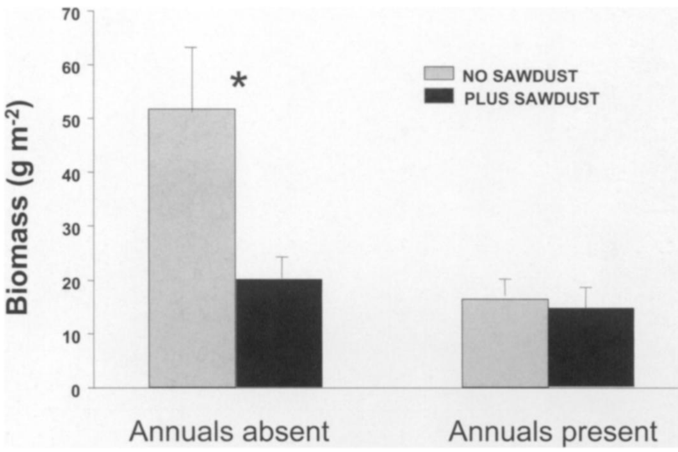

Figure 2. Growth response of red fescue with and without sawdust addition, in the presence or absence of annual grass competition at the end of the 2000 growing season. Bars represent means ± 1 SE (N = 7). An "*" denotes a significant effect of sawdust addition ($P < 0.05$).

gests that although broom effects on soil N may be large in some sites, there are perhaps other sites where broom effects will be negligible or small. From a management perspective, it is important to distinguish sites where invaders will have minor effects from those where they may have large effects to prioritize removal and restoration efforts (Parker et al. 1999).

The results of the leaf ^{15}N survey that we conducted are consistent with the prediction for N-fixers compared with non–N-fixers. Non–N-fixers should have a wider range of leaf ^{15}N values, compared with the fixers (if the fixers are indeed fixing) (Virginia and Delwiche 1982). Coyote bush, our reference non–N-fixing shrub, had a wider range of ^{15}N values around zero, whereas the brooms were relatively more clustered around zero, in comparison. Of the two brooms, French broom appeared to be more reliant on fixation compared with Scotch broom because its leaf ^{15}N values were more clustered around zero (at least at five of the eight sites) than those of Scotch broom. These results, coupled with higher %N in broom leaf tissue, suggest that the brooms are accessing different N than the reference non–N-fixer (i.e., fixing N). However, at some of the sites, broom leaf ^{15}N values were higher and more similar to the non–N-fixer. These responses may suggest that in those sites, there is a shift away from reliance on fixation and a similar N source for all individuals (Stock et al. 1995). At sites like this, fixation may not be important because of abundant available N or lack of available phosphorus, a critical factor in N fixation. Effects by broom on soil properties in these sites may consequently be low.

At two of our sites (Johnson Prairie in Washington, and Oakwood Valley in California), however, the changes in soil N availability with invasion that we document are quite large. In both sites, increases in net N mineralization were up to three times greater in broom-invaded soil compared with uninvaded soil. At the same time, however, the total N pool itself (which includes both available and refractory, or unavailable, N) does not appear to be altered as dramatically. We observed only a slight (~6%) increase in total soil N from uninvaded to broom-invaded soil in Washington. This finding is consistent with the findings of Binkley et al. (1985) in a red-alder system in the Pacific Northwest; they suggest that N-fixers may cause larger changes in N cycling rates than in the total N capital of a system.

The growth of our greenhouse bioassay species, yarrow, points to a whole new component of broom effects that might have important implications for restoration after broom removal. *Achillea* grew almost a third smaller in broom-invaded soils compared with uninvaded, suggesting the presence of an inhibitory compound in broom soils. For example, quinolizidine alkaloids are produced as defensive compounds by Scotch broom and have been shown to have inhibitory effects on germination and protein synthesis in some herbaceous species (Wink and Twardowski 1992; Wink et al. 1983). In other words, Scotch broom may cause increases in available soil N, but this N may not be accessible to all species. In fact, some species may be inhibited by certain compounds produced by Scotch broom.

Although a number of methods for broom removal exist, burning appears to be a particularly efficient one. In addition to the obvious effect of aboveground biomass removal, our results suggest that repeated burns not only reduce the seedbank but may also decrease total N in the surface soils (up to 40%). In sites that have been burned, then, managers may not have to deal with the issue of elevated N (or a "fertilization effect" of broom). However, burning is not always feasible. In many sites, manual methods such as cutting or pulling may be the only option. In those cases, elevated N levels may need to be addressed before site revegetation can occur. Many studies have shown that in sites where N-fixers have been removed or diedback, weedy species dominated the site (Adler et al. 1998; Maron and Connors 1996; Mueller-Dombois and Whiteaker 1990). The addition of a C source such as sawdust to the soil may trigger a N-uptake response among soil microbes, which may effectively keep N from the plants. This management input would seem to be a reasonable approach to lowering elevated N in broom-removal sites. Our results suggest, however, that although it is possible to cause a decrease in plant-available N in surface soils, it is difficult to target the particular group of species. In our study, the supposedly slow-responding native red fescue responded as strongly to sawdust addition as we predicted annual grasses would respond.

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