

## Soil changes accompanying invasion of the exotic shrub *Cytisus scoparius* in glacial outwash prairies of western Washington [USA]

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### Abstract

Shrub encroachment of grassland is a global phenomenon that can cause substantial and rapid changes in soil nutrient levels and distribution. If the woody plants in question also have the capacity to fix nitrogen (N), the effects on soil nutrients may potentially be large. *Cytisus scoparius* L. Link (Scotch broom) is an introduced leguminous shrub from the Mediterranean region that colonizes open grasslands. We measured several properties of the surface soil (0–10 cm depth) across advancing fronts of *Cytisus* to assess changes in soil fertility associated with invasion in western Washington state (USA). Both total soil C and N increased (1.8% and 6.5%, respectively), resulting in a decrease in C to N ratio of 22.5 in uninvaded soils to 21.5 inside *Cytisus* patches.  $\delta^{15}\text{N}$  signature of surface soil did not clearly demonstrate a signal of N<sub>2</sub>-fixation across the *Cytisus* gradient. On the other hand, seven-day laboratory aerobic incubations demonstrated 3 and 2.4 times greater mineralization and nitrification rate, respectively, in *Cytisus* soils compared to uninvaded soils. Despite this increase in N availability, bioassay plants (*Achillea millefolium*) grown in uninvaded soils in the greenhouse were ~30% larger than those grown in *Cytisus*-invaded soils, suggesting that *Cytisus* may have inhibitory effects on some plants growing in invaded soils. These results suggest that the impact of *Cytisus* invasion on grassland plant communities may be influenced or tempered by chemical or microbial effects on the soil other than simply increased labile N.

### Introduction

Woody plant abundance has increased substantially in arid and semiarid grasslands and savannas worldwide over the last 50 to 300 years (Archer, 1989). The mechanisms responsible for this shift in vegetation remain controversial but are likely a combination of changes in climate, fire frequency, and grazing (Archer et al., 1988). Rapid and substantial changes in soil fertility associated with these species replacements have been documented (e.g., Chapela et al., 2001; Hibbard et al., 2001; Alfredsson et al., 1998; Bashkin and Binkley, 1998; Davis, 1995). Nitrogen-fixing (N<sub>2</sub>-fixing) plants are disproportionately repre-

sented among invaders of natural areas globally (Daehler, 1998), with many occurring in sites undergoing this grassland-to-woodland conversion process [e.g., *Prosopis* in southwestern US (Van Auken and Bush, 1988), *Acacia spp.* in South Africa fynbos and strandveld (Witkowski, 1991) and *Mimosa pigra* in North Australian savannas (Lonsdale and Miller, 1993)]. Changes in soil fertility with invasion may be different with N<sub>2</sub>-fixing shrubs than with non-fixing shrubs. Because leaf N concentration of N<sub>2</sub>-fixers typically is higher than non-fixing plants (McKey, 1994), decomposition could be released from N-limitation (Berg et al., 1995), potentially leading to changes in soil C and N accumulation. For example,

if decomposition rates are accelerated, increased microbial consumption of soil organic matter could reduce belowground C pools (Berg et al., 1995). The purpose of this study was to evaluate and quantify the effect of an introduced N<sub>2</sub>-fixing shrub on surface soil C and N accumulation and turnover as it invades a grass-dominated ecosystem.

*Cytisus scoparius* (Scotch or Scot's broom, hereafter *Cytisus*) is presently invading a number of natural areas on the west coast of North America, including open grasslands and the understory of Douglas fir (*Pseudotsuga menziesii*) forests. It occurs additionally in disturbed urban areas, such as parks and landfills. In glacial outwash prairies of western Washington, where we conducted this investigation, stands of the large woody *Cytisus* are replacing a grassland community dominated by *Festuca idahoensis* and small herbaceous perennials such as *Camassia quamash* and *Aster curtis*. This invasion is correlated with a decrease in native species diversity (Parker et al., 1997), and is occurring more rapidly in undisturbed prairies than in areas such as urban parks that have experienced high levels of anthropogenic influence (Parker, 2000).

We assessed the impacts of *Cytisus* on soils by sampling soils along transects from dense *Cytisus* patches, across the advancing front of patches, into uninvaded grassland. We hypothesized that the effect of *Cytisus* would be a function of its density or biomass, as well as how long a particular point had been invaded (using space as a proxy for time). Our approach had two components: first, we characterized the size of total C and N pools along *Cytisus*-to-grass transects and ascertained whether the total N pool contained any N<sub>2</sub>-fixation signal. We predicted that along a *Cytisus*-to-grass gradient, the total soil N pool should increase more than the total C pool, resulting in a lower C:N ratio in *Cytisus*-invaded soils which would reflect differences in both standing above-ground biomass and litter quality. We also predicted that the  $\delta^{15}\text{N}$  signal of the total N pool in *Cytisus*-invaded soils would more closely reflect that of the atmosphere (0.3663 ‰, expressed by convention as 0 ‰) compared to uninvaded soils due to deposition of <sup>15</sup>N-depleted litter material. A lower <sup>15</sup>N value in *Cytisus*-invaded compared to uninvaded soils would provide indirect evidence of N<sub>2</sub>-fixation by *Cytisus*. Second, we measured the active portion of the total N pool, that is, the fraction that is most readily mineralized by soil microbes and thus available to plants. Here we hypothesized that plant-available N would

be increased in *Cytisus*-invaded soils compared to uninvaded soils and that this could benefit understory herb species. We tested this hypothesis with a laboratory assay for mineralizable N and a greenhouse bio-assay of seedling growth of a common herb in *Cytisus*-invaded and uninvaded soils (Binkley and Hart, 1989).

## Materials and Methods

### Study site

Johnson Prairie is located on the Fort Lewis Military Reservation (46°55' N 123°16'W), Washington, approximately 80 km south of Seattle in the Puget Sound trough. The climate is characterized by mild temperatures with narrow diel fluctuations (6-10° C) (Franklin and Dyrness, 1988). The winters are wet and mild; summers relatively dry and cool. Average annual precipitation is 888 mm, 75-85% of which occurs October 1 – March 31. Average January minimum temperature is 1.1°C; average July maximum is 24.1°C (Franklin and Dyrness, 1988). Soils are coarse-textured Andisols and Inceptisols, containing high amounts of charcoal due both to historical burning by native Americans and by current burning that is used to control *Cytisus* and Douglas fir (*Pseudotsuga menziesii*). These prairies are dominated by *Festuca idahoensis* and include small herbaceous perennials such as *Camassia quamash* and the state-threatened *Aster curtis*, with intervening space covered by a thick cryptogamic layer (Lang, 1961). According to aerial photos, *Cytisus* began to invade Johnson Prairie in the 1940's (Parker, unpublished data), but was kept in check by regular burning until this was interrupted after 1982. Following the cessation of prescribed fire, resource managers at Fort Lewis observed significant spread of *Cytisus* into uninvaded terrain (J. Reasoner, Department of Forestry, Fort Lewis, personal communication). At the time of our study, the prairie was a patchwork of open areas and small *Cytisus* stands, most of which were probably 10-15 years old. Patches of *Cytisus* in Johnson Prairie range in size from several individuals to upwards of thousands of individuals, with patch diameters as large as ~200 m.

### Soil collection and *Cytisus* stand sampling

In December 1996 we randomly chose 18 *Cytisus* stands that were at least 20 m in diameter. One of four cardinal directions was chosen at random to select the side of the *Cytisus* stand to be sampled. We identified the stand edge, where *Cytisus* density was between one-two individuals per square meter (Table 1). 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. At each interval, we sampled *Cytisus* density within a 1-m radius around the core location. We measured branch number and diameter for each individual and calculated *Cytisus* biomass per square meter using an algorithm determined previously from the same site by Parker (1996).

All soils were stored at 4°C until total C, total N, and  $\delta^{15}\text{N}$  signature analyses were conducted. In order to have fresh samples for laboratory and greenhouse assessment of N availability, a second collection of soil was taken in April, 1997. At that time twelve of the original 18 *Cytisus* patches were randomly selected, and 20 cm diameter cores from the surface 10 cm of soil were collected within *Cytisus* infestations at approximately 9 m in from edge and within adjacent, uninvaded grassland at least 9 m from an edge. Soils were transported back to the laboratory at UC Berkeley in coolers.

### Analysis of total soil C, N, and $\delta^{15}\text{N}$

Soils were dried for 48 h at 65°C, passed through a <2mm sieve, then finely ground with mortar and pestle. Samples were then analyzed for total C and total N by combustion on a Carlo Erba NA 1500 CHN analyzer (Fisons Instruments, Beverly, Massachusetts, USA). Separate samples were analyzed for  $^{15}\text{N}$  natural abundance at the Stable Isotope Facility at University of California, Davis. We used standard delta notation to express the natural abundance of  $^{15}\text{N}$  (Shearer and Kohl, 1989).

### Laboratory and greenhouse assays of N availability

After the second soil collection, incubations were begun within four days. Directly before analysis, soils were removed from 4°C storage and homogenized by hand. Large rocks, charcoal, and organic material >

Table 1. Selected patch and soil characteristics (top 15 cm) at seven points along 18 m transect running perpendicular to advancing front of *Cytisus* infestation (-9m = grassland; to 9m = center of *Cytisus* patch). Values are means (N = 18), followed by 1 standard deviation in parentheses.

Location along transect:	-9m	-6m	-3m	0m	3m	6m	9m
Average basal diameter (cm)	0.95 (4.03)	3.21 (4.90)	7.37 (7.65)	15.2 (11.5)	18.8 (8.92)	21.8 (5.58)	20.3 (5.92)
Density (# indivs/m <sup>2</sup> )	0.04 (0.10)	0.16 (0.27)	0.57 (0.57)	1.63 (1.33)	2.69 (2.35)	2.72 (1.65)	3.15 (2.13)
Total aboveground biomass (g/m <sup>2</sup> )	58.2 (230)	47.5 (116)	386.1 (649)	1635.1 (1601)	3588.9 (2255)	5852.1 (3276)	5578.8 (1776)
Total N (g/m <sup>2</sup> )	427.1 (85.31)	425.84 (103.08)	443.44 (61.99)	378.94 (99.95)	496.34 (113.96)	469.28 (136.19)	454.67 (120.16)
Total C (g/m <sup>2</sup> )	9117.5 (1769.6)	9096.1 (2200.7)	9511.31 (1250.0)	8057.97 (2055.0)	10415.4 (2357.0)	9739.31 (2712.9)	9339.7 (2294.1)
C:N	21.52 (0.58)	21.40 (1.03)	21.49 (0.75)	21.47 (1.05)	21.03 (1.05)	20.83 (0.66)	20.65 (0.72)
$\delta^{15}\text{N}$	3.62 (0.84)	3.32 (0.49)	3.54 (0.35)	3.98 (1.49)	3.59 (0.96)	3.52 (0.65)	3.55 (0.58)

2mm was removed. Two subsamples of approximately 15 g wet weight were taken from each core; one was immediately extracted in 50 mL 2 M KCl. The other set of subsamples was incubated at room temperature (22°C) for seven days, after which they were extracted. Another subsample of soil was weighed, dried at 105°C for 24h then reweighed, for correction of soil weight using gravimetric water content. All samples for N extraction were shaken for 30 minutes immediately following KCl addition and filtered through Whatman #1 filters that had been pre-leached with deionized water. Extractants were then frozen until colorimetric analysis on a Lachat Flow-injection Autoanalyzer, using QuikChem Method No. 12-107-06-2-A and 12-107-04-1-B for  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , respectively. Net nitrogen mineralization and net nitrification rates were calculated by subtracting final  $(\text{NH}_4^+ + \text{NO}_3^-)\text{-N}$  and  $\text{NO}_3^- - \text{N}$  concentrations, respectively, from those in pre-incubation samples. All rates are expressed on a per gram dry soil basis (105°C for 24h).

For the greenhouse bioassay, soil cores from *Cytisus*-invaded and uninvaded grassland were composited separately. Composited soils were then evenly distributed into 110 four-inch plastic pots ( $n = 55$  for each soil type). Each pot received four seeds of *Achillea millefolium*, a common herbaceous perennial that occurs in Johnson prairie. Approximately six weeks after planting, germination on all pots was censused and the number of seedlings randomly reduced to two; four weeks subsequently all pots were thinned to a single individual. Eight weeks after thinning, all pots were harvested and soil gently washed from roots. Plants were snipped with scissors at the shoot/root interface, each part dried at 65°C for 48 h, then weighed. Final sample sizes reflect loss of some replicates due to seedling mortality.

#### Statistical analyses

Total soil C, N and  $\delta^{15}\text{N}$  signatures along the grass-to-*Cytisus* transect were analyzed using linear regression, with *Cytisus* biomass as the independent variable. Paired t-tests were used to compare differences in net mineralization and nitrification rates between *Cytisus*-invaded and uninvaded soils. Unpaired t-tests were used to test for differences between *Cytisus*-invaded and uninvaded soils in percent emergence, aboveground biomass, root biomass, and root:shoot ratios of *Achillea* individuals. *Achillea* biomass was log-transformed before analysis. All statistical

analyses were conducted with SYSTAT 7.0 (SYSTAT 1997).

#### Results

*Cytisus* density increased from 0.04 individuals  $\text{m}^{-2}$  (SE = 0.02) in grassland to 3.15 individuals  $\text{m}^{-2}$  ( $\pm 0.50$ ) in center of *Cytisus* patches (Table 1). At the uninvaded end of transects, we encountered only two *Cytisus* individuals across the 18 transects. Estimated *Cytisus* aboveground biomass increased from 58.2  $\text{g m}^{-2}$  ( $\pm 230$ ) in uninvaded grassland to 5578  $\text{g m}^{-2}$  ( $\pm 1776$ ) at the opposite end of the transect, approaching the center of infestations (Table 1).

Total N pool increased by less than 30  $\text{g m}^{-2}$  across the grass-to-*Cytisus* gradient (Table 1); this increase was statistically significant, although biomass explained little variance in total N (Figure 1;  $R^2 = 0.07$ ;  $P = 0.003$ ;  $N = 126$ ; Nitrogen =  $0.42 + 9.3 \times 10^{-6} * \text{Biomass}$ ). Total C pool increased slightly ( $\sim 2\%$ ) across the gradient (Table 1). As with total N, the relationship between C and biomass was significant but explained little variance ( $R^2 = 0.04$ ;  $P = 0.03$ ;  $N = 126$ ; Carbon =  $9.0 + 1.4 \times 10^{-4} * \text{Biomass}$ ). These two pool changes then resulted in a small decrease in the C to N ratio from uninvaded to *Cytisus*-invaded soils (Table 1). *Cytisus* biomass significantly predicted C:N (Figure 1;  $R^2 = 0.190$ ;  $P < 0.0005$ ;  $N = 125$ ; C:N =  $21.5 - 0.001 * \text{Biomass}$ ).

Natural abundance  $^{15}\text{N}$  signature of the surface soil appeared to decrease slightly as a function of *Cytisus* biomass (Figure 2). However, the values across the transect remained virtually the same (Table 1) and were not statistically related to biomass ( $R^2 = 0.009$ ;  $P = 0.32$ ;  $N = 116$ ).

Net mineralization and nitrification rates were significantly higher in *Cytisus*-invaded compared to non-invaded soils ( $df = 11$ ,  $t = 4.062$ ,  $P = 0.002$  for mineralization and  $df = 11$ ,  $t = 3.345$ ,  $P = 0.007$  for nitrification;  $N = 12$ ) (Figure 3). There was a trend toward nitrification accounting for a greater percentage of the N mineralized in uninvaded soils (89.3%) compared to *Cytisus*-invaded soils (73%) ( $df = 11$ ,  $t = 1.648$ ;  $P = 0.128$ ). The gravimetric water content of *Cytisus* and grass soils was 34.1% ( $\pm 2.2\%$ ) and 32.9% ( $\pm 6.1\%$ ) respectively, a difference that was not statistically significant ( $df = 11$ ,  $t = 0.07$ ;  $P = 0.945$ ).

In the greenhouse bioassay, both aboveground and belowground components of *Achillea* were  $\sim 30\%$

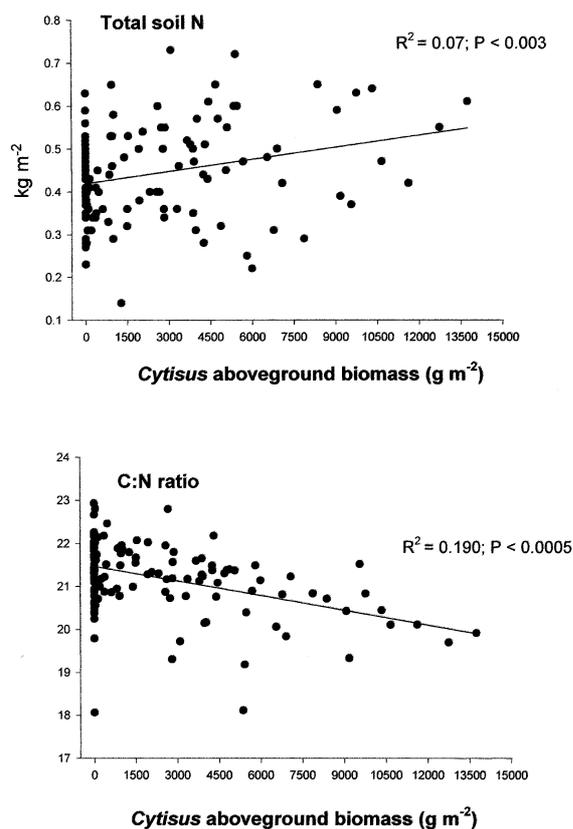


Figure 1. Top panel: Total soil nitrogen (N) of surface soil (0-15 cm depth) (plant litter material or organic horizon excluded) as a function of *Cytisus* biomass along an 18 m transect that runs perpendicular to advancing front of *Cytisus*, from uninvaded grassland (-9 m) into dense *Cytisus* stands (9 m). Bottom panel: Carbon-to-nitrogen (C:N) ratio of surface soil (0-15 cm depth) as a function of *Cytisus* biomass along same transect.

larger in grass soils compared to *Cytisus* soils, a significant increase (Table 2). There was no significant difference between soil types in root:shoot ratio of *Achillea* or percent seedling emergence (Table 2).

## Discussion

### Total C, N pools and $\delta^{15}\text{N}$ signature

Total C and N pools of the surface soils increased only slightly across the invasion front, resulting in a concurrent decrease in C:N ratio of less than one unit. Others report similarly small decreases associated with N<sub>2</sub>-fixers (e.g., Kaye et al., 2000), but such changes are dramatically smaller than those reported

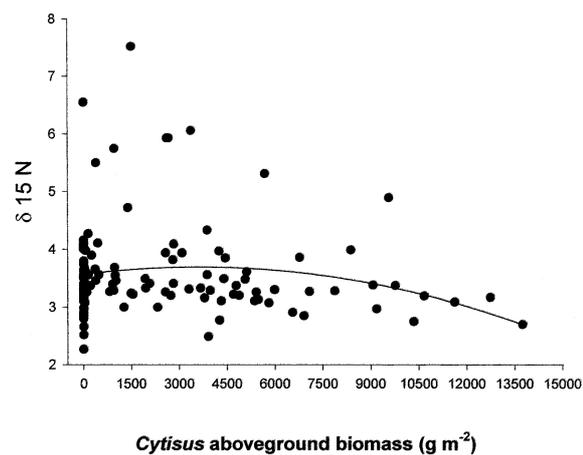


Figure 2. Natural abundance ( $\delta^{15}\text{N}$ ) signature of surface soil (0-15 cm depth) (organic horizon excluded) as a function of *Cytisus* biomass along 18 m transect that runs perpendicular to advancing front of *Cytisus*, from uninvaded grassland into dense *Cytisus* stands.

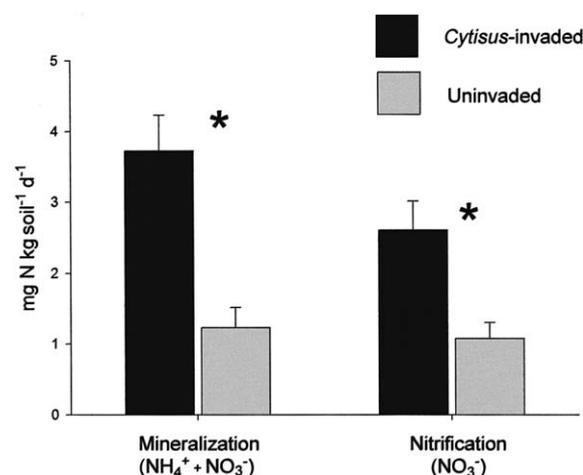


Figure 3. Net nitrogen mineralization (NH<sub>4</sub><sup>+</sup> + NO<sub>3</sub><sup>-</sup>) and nitrification (NO<sub>3</sub><sup>-</sup>) rates in surface soils (0-15 cm depth) of glacial outwash prairie (uninvaded and *Cytisus*-invaded) ecosystems, as determined in 7-d laboratory aerobic incubations. Values are means  $\pm$  1 SE (n = 12). \* indicates significant differences between soil types (mineralization and nitrification analyzed separately) (paired t, P < 0.05).

by Stock et al (1995). In that study, invasion by the N<sub>2</sub>-fixer *Acacia saligna* into South African fynbos habitat resulted in C:N decrease of 35.2 to 25.6, and a smaller though still substantial decrease from 20.6 to 16.2 in nearby strandveld systems that were invaded by *Acacia cyclops*. In these systems, the change in C:N is driven more by increased soil N under *Acacia* spp. than increased soil organic matter (Stock et al., 1995). This is consistent with our

Table 2. Seedling emergence (%) and biomass (g) of shoot, bolt, root and root:shoot ratio of *Achillea* in *Cytisus*-invaded and uninvaded soils. Values are means  $\pm$  1 standard deviation in parentheses.

Measure:	Cytisus-invaded soil			Uninvaded soil			t	P
	Mean	St dev	N	Mean	St dev	N		
Seedling Emergence (%)	69	(24)	54	65	(28)	54	0.72	0.470
Shoot	0.76	(0.46)	51	1.00	(0.45)	50	2.70	0.008
Root	0.43	(0.26)	51	0.58	(0.27)	50	2.46	0.016
Root:Shoot Ratio	1.78	(0.47)	51	1.85	(0.56)	50	0.51	0.610

results, where the change in C:N was due more to a change in total N over the transect (an increase of ~6% in the total pool) rather than total C (a change of ~1%). It is possible that total pool sizes will be more strongly altered by *Cytisus* as time passes. Others have shown that depending on the nature of the woody plant patch replacing the herbaceous habitat, accretion of C and N can be remarkably slow (e.g., Hibbard et al., 2001). The *Acacia* soils sampled by Stock et al. (1995), which showed such dramatic declines in C:N, had been invaded for up to 30 years. Alternatively, regular burning in these prairies may result in losses of both C and N from soils (e.g., Mack et al., 2001; Roscoe et al., 2000; Garcia-Oliva et al., 1999), which may obscure effects of *Cytisus*.

Natural abundance  $^{15}\text{N}$  of soils across the transects did not differ significantly, although the trend suggests a decreasing response from uninvaded to *Cytisus*-invaded soils (Figure 2). Although we do not have  $\delta^{15}\text{N}$  foliar values for *Cytisus* itself at this site, related work in coastal California demonstrated that *Cytisus* foliage tends to be about zero (range = 0.12 to 1.46‰; Haubensak, 2001). We would therefore expect that the  $\delta^{15}\text{N}$  values of the soil would become diluted (more depleted) over time as more of this depleted litter material is received. This effect should be enhanced even further because grasses (as in the uninvaded soils) tend to be more enriched in  $^{15}\text{N}$  than woody and long-lived plants (Virginia and Delwiche, 1982). However, this pattern would only be expected if *Cytisus* is the sole source of fixed N.

The similarity in  $^{15}\text{N}$  values across the gradient may suggest other sources of  $\text{N}_2$ -fixation. Cover of cryptogamic crusts decreases as *Cytisus* invades (Parker, unpublished data). If these crusts contain blue-green algae and fix substantial N, there might be a shift in  $\text{N}_2$ -fixation source with invasion (from crust to *Cytisus*) but no net change in soil isotope value. Alternatively, *Cytisus* itself may change its dependence on  $\text{N}_2$ -fixation as invasion occurs.  $\text{N}_2$ -fixation

may be more important at the edge of the invasion front where *Cytisus* individuals are smaller and competition with resident species most intense. As *Cytisus* individuals grow larger and produce greater quantities of N-rich litterfall, availability of mineral N may increase. Thus, uptake of mineral N may become more important for *Cytisus* than  $\text{N}_2$ -fixation as the invasion proceeds. In this scenario, varying dependence on  $\text{N}_2$ -fixation across the *Cytisus*-to-grass gradient might result in little overall change in isotopic signatures as well.

While a number of others have used differences in soil  $^{15}\text{N}$  signatures between putative  $\text{N}_2$ -fixers and non- $\text{N}_2$ -fixers as supporting evidence that  $\text{N}_2$ -fixation is an N source (e.g., Binkley et al., 1985; Stock et al., 1995; Virginia and Delwiche 1982; Piccolo et al., 1996), the literature overall is ambiguous. For example, Hansen and Pate (1987) found no consistent differences in  $^{15}\text{N}$  natural abundance values between foliage of putative  $\text{N}_2$ -fixing plants and non- $\text{N}_2$ -fixing plants in Australian jarrah (*Eucalyptus*) forest. Shearer et al. (1983), similarly, found that total soil  $\delta^{15}\text{N}$  was not different under versus away from the apparently  $\text{N}_2$ -fixing tree legume, *Prosopis juliflora*. Even in stands of red alder (*Alnus rubra*), where fixation rates can be up to 300 kg ha<sup>-1</sup>, Binkley et al. (1985) reported no significant difference in  $\delta^{15}\text{N}$  of either foliage or soil N in alder stands compared to mixed conifer stands. Therefore, the lack of a significant effect of *Cytisus* aboveground biomass on the isotopic signature of soils that we report does not necessarily refute our hypothesis that *Cytisus* affects soil N status by  $\text{N}_2$ -fixation.

#### *N* availability

In the second part of this study, we characterized the active, or labile, fraction of the total N pool in *Cytisus*-invaded versus uninvaded soils. When soils were assayed under field moist conditions and con-

stant temperature, net nitrogen mineralization and nitrification rates were 3 and 2.4 times greater, respectively, in *Cytisus*-invaded compared to uninvaded soil. Differences in moisture levels between soils cannot explain differences between soils, since gravimetric water contents of the two soils were similar. Therefore, it is very likely that the increases in N mineralization and nitrification rates were driven by increases in substrate quality provided by *Cytisus*. This soil N enhancement effect has been demonstrated in a number of other studies of N<sub>2</sub>-fixers [e.g., *Acacia cyclops* (Stock et al., 1995), *Lupinus arboreus* (Maron and Connors, 1996) and *Myrica faya* (Vitousek and Walker 1989)] as well as non-N<sub>2</sub>-fixers (Hibbard et al., 2001). Enhancement of soil N quality by N<sub>2</sub>-fixers may appear to be highly predictable, yet this effect can vary strongly even between closely related species. For example, Stock et al. (1995) found that while abundant *Acacia cyclops* increased N mineralization rates three- to five-fold, its equally abundant congener *A. saligna* had no discernible effect on soil N and P mineralization in adjacent habitat.

In contrast to the laboratory assay (absent plant uptake), the greenhouse bioassay with *Achillea millefolium* integrated the response of both mineralizing microbes and plants. Increased plant growth in *Cytisus*-invaded soils would have corroborated the laboratory assay; instead, we observed decreased plant growth in *Cytisus*-invaded soils by up to 30%. This suggests that *Cytisus* may cause changes in soils that are independent of nutrient status. First, the quinolizidine alkaloids produced as defensive compounds by *Cytisus* have been shown to have inhibitory effects on germination and protein synthesis in some herbaceous species (Wink et al., 1983; Wink and Twardowski, 1992). Second, changes in soil microbial communities that may occur with *Cytisus* invasion could affect plant growth; for example, *Cytisus*-invaded soils may lack a particular mycorrhizal fungus partner of *Achillea* (Koomen et al., 1987; Ronsheim and Anderson, 2001). Our result may only reflect an idiosyncratic response of *Achillea*, underscoring a problem with using bioassays for determining plant N availability: the choice of response species may greatly influence the outcome (Binkley and Hart, 1989). In fact, in an unpublished study, Maron found an increase in growth of barley planted in *Cytisus*-invaded soil compared to uninvaded soil from a disturbed grassland site in Washington (J. Maron, pers. com.). Nonetheless, our result suggests that elevated N availability as affected by *Cytisus* may not

be immediately accessible to other species. Further, the response of the resident plant community to soil changes associated with *Cytisus* invasion may be idiosyncratic and difficult to predict.

The fact that we observed small changes in total pools but large changes in active pools is consistent with the results of Wedin and Pastor's (1993) study of grasses in monocultures and their subsequent effects on soil nutrients. They reported that if species affect the most labile fraction of the total pool, changes can be small and still have large implications for nutrient availability. More generally, our results suggest that there may be changes associated with *Cytisus* invasion even if N inputs are not significantly increased, or if changes are not directly linked to N<sub>2</sub>-fixation. This is consistent with the observation by Binkley et al. (1985) that N<sub>2</sub>-fixers typically accelerate N turnover more than they increase N capital. In order to understand whether these nutrient changes associated with *Cytisus* invasion can have important plant community implications, we must have information on the individual responses of species associated with *Cytisus*. Many N<sub>2</sub>-fixers are associated with weedy species because faster-growing species can exploit nutrient richness more quickly than slower-growing species; this effect is typically not observed until die-back of the N<sub>2</sub>-fixer occurs, however [e.g., *Myrica faya* (Mueller-Dombois and Whiteaker, 1990, Adler et al., 1998) and *Lupinus arboreus* (Maron and Connors, 1996)]. *Cytisus* invasion at these prairie sites is associated with a decline in native species richness and cover, with a shift from native species to weedy exotic grasses and forbs such as *Agrostis tenuis*, *Holcus lanatus*, and *Hypochaeris radicata* (Parker et al., 1997). It is possible both that the nutrient enhancement and the potentially negative effects that we found in *Cytisus*-invaded soils play a role in this shift in community composition with invasion.

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