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EXOTIC PLANT INVASION ALTERS NITROGEN DYNAMICS IN AN ARID GRASSLAND

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Abstract. The introduction of nonnative plant species may decrease ecosystem stability by altering the availability of nitrogen (N) for plant growth. Invasive species can impact N availability by changing litter quantity and quality, rates of N_2-fixation, or rates of N loss. We quantified the effects of invasion by the annual grass *Bromus tectorum* on N cycling in an arid grassland on the Colorado Plateau (USA). The invasion occurred in 1994 in two community types in an undisturbed grassland. This natural experiment allowed us to measure the immediate responses following invasion without the confounding effects of previous disturbance. Litter biomass and the C:N and lignin:N ratios were measured to determine the effects on litter dynamics. Long-term soil incubations (415 d) were used to measure potential microbial respiration and net N mineralization. Plant-available N was quantified for two years in situ with ion-exchange resin bags, and potential changes in rates of gaseous N loss were estimated by measuring denitrification enzyme activity. *Bromus* invasion significantly increased litter biomass, and *Bromus* litter had significantly greater C:N and lignin:N ratios than did native species. The change in litter quantity and chemistry decreased potential rates of net N mineralization in sites with *Bromus* by decreasing nitrogen available for microbial activity. Inorganic N was 50% lower on *Hilaria* sites with *Bromus* during the spring of 1997, but no differences were observed during 1998. The contrasting differences between years are likely due to moisture availability; spring precipitation was 15% greater than average during 1997, but 52% below average during spring of 1998. *Bromus* may cause a short-term decrease in N loss by decreasing substrate availability and denitrification enzyme activity, but N loss is likely to be greater in invaded sites in the long term because of increased fire frequency and greater N volatilization during fire. We hypothesize that the introduction of *Bromus* in conjunction with land-use change has established a series of positive feedbacks that will decrease N availability and alter species composition.

Key words: Bromus tectorum; *Canyonlands National Park, Utah, USA; denitrification enzyme activity; desert vegetation; ecosystem carbon; ecosystem nitrogen; grasslands; invasive species; litter, changes in biomass and chemistry; N mineralization; plant-available N following plant invasion; plant invasion, litter quality.*

INTRODUCTION

Invasion by nonnative species represents one of the most significant components of global change (Vitousek et al. 1997). Plant invasions can decrease ecosystem stability by altering resource supply, changing trophic structure and relationships, or by facilitating disturbance (Vitousek 1990). Soil nitrogen is one of the most important factors that determine ecosystem stability (Chapin et al. 1996), and the introduction of a single species can have large effects on rates of nitrogen transformations by changing litter quality and quantity (Wedin and Tilman 1990, Hobbie 1992, Wedin and Pastor 1993, Vinton and Burke 1995, 1997). Invasive species can also increase soil N through N_2-fixation (Vitousek et al. 1987, Vitousek and Walker 1989), or alternatively, decrease soil N by increasing fire frequency and N loss (Hughes et al. 1991, D'Antonio and Vitousek 1992, Ley and D'Antonio 1998, Mack and D'Antonio 1998).

One of the most significant plant invasions in North America has been the establishment of *Bromus tectorum* L. (hereafter referred to as "*Bromus*") in arid regions of the intermountain West (Mack 1981, D'Antonio and Vitousek 1992, Vitousek et al. 1997). *Bromus* was first observed in the late 1890s at locations in Washington, Oregon, and Utah (Mack 1981). It reached its current range of ~40 000 000 ha by 1930 and may now be the dominant plant in this region (Mack 1981). The success

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of *Bromus* has been attributed to four factors. First, ecosystems in this region evolved in the absence of grazing (Mack and Thompson 1982). Vegetation in pristine sites is characterized by bunchgrasses or shrubs with a biological soil crust covering intercanopy spaces (West 1988). Both the vegetation and soil crust are intolerant of grazing (Mack and Thompson 1982, Knapp 1996). Extensive land-use change that began in the 1800s eliminates competition from native species and creates open areas for *Bromus* establishment (Mack 1981, Knapp 1996, Smith et al. 1997). Second, *Bromus* exhibits a high degree of phenotypic plasticity in life-history characteristics that allows for production of large numbers of seeds during favorable conditions yet ensures some seed production in unfavorable years (Mack and Pyke 1983, Rice and Mack 1991, Rice et al. 1992). Third, *Bromus* develops an extensive root system during fall and winter that allows it to outcompete native species whose root growth is primarily during spring (Harris 1967, Dobrowolski et al. 1990). Fourth, *Bromus* increases fire frequency to a point where native species can no longer survive (Klemmedson and Smith 1964, Whisenant 1992, Brandt and Rickard 1994, Knapp 1996).

The pattern of *Bromus* invasion is among the best understood of any invasive species (Mack 1981, 1986, D'Antonio and Vitousek 1992, Vitousek et al. 1997), yet little is known on how invasion alters N and C cycling. Rimer (1998) observed that *Bromus* decreased the size of the labile N pool, mineralization potential, and soil inorganic N only two years after invasion of undisturbed sites on the Colorado Plateau. Bolton et al. (1990) found that mineralization potentials for *Bromus* stands were greater than native shrub communities in the shrub-steppe, but lower than native grass communities. Microbial biomass C and N and soil respiration were also greatest in *Bromus* stands (Bolton et al. 1993). Fires that often accompany *Bromus* invasion can decrease total soil N and increase the soil C:N ratio (Blank et al. 1994, Halvorson et al. 1997).

The goal of this study was to quantify the changes in the N cycle that occur immediately following the establishment of *Bromus tectorum*. We believe there are two unique aspects of this study. First, we are studying a recent invasion that occurred in a location that has served as a study site for N dynamics in arid lands for the past three decades (Kleiner and Harper 1972, 1977, Evans and Belnap 1999), so the date of the invasion is known. Second, invasion of *Bromus* often occurs after disturbance because germination is enhanced following removal of the biological soil crust (Daubenmire 1970, Mack and Thompson 1982). This study examines the effects of invasion in undisturbed grasslands so the potential confounding effects of disturbance are not present. The objectives were to quantify the changes that occur immediately following invasion in (1) litter quantity and chemistry, (2) potential mineralization, microbial respiration, and denitrification, and (3) plant-available N.

METHODS

Study site

The study site was located in Virginia Park (38°05′ 43″ N, 109°50′31″ W) within the Needles District of Canyonlands National Park, Utah, USA. Annual precipitation is 21.4 cm with 18, 25, 27, and 30% occurring during the winter, spring, summer, and fall climatological seasons, respectively (Western Regional Climate Center, Reno, Nevada, USA). Virginia Park is a grassland of 97 ha that has never been grazed due to inaccessibility (Kleiner and Harper 1972). The vegetation is characterized by perennial bunchgrasses including *Hilaria jamesii* (Torr.) Benth., *Stipa comata* (Trin. & Rupr.), *Stipa hymenoides* (R&S) Ricker, and *Sporobolus cryptandrus* (Torr.) Gray. Soils are part of the Begay series and are classified as coarse-loamy, mixed, mesic Ustollic Camborthids (Lammers 1991). Complete plant and soil descriptions are found in Kleiner and Harper (1972). Nomenclature for all species follows Welsh et al. (1987). Plant interspaces are dominated by a biological soil crust (Kleiner and Harper 1972). Nitrogen fixation by lichens and cyanobacteria within the crust is the dominant source of N input into this ecosystem (Evans and Ehleringer 1993, 1994, Evans and Belnap 1999, Evans and Lange 2001). *Bromus* has existed in Utah since the late 1800s (Mack 1981), however it was not a conspicuous member of the grassland communities in Virginia Park until 1994 (Kleiner and Harper 1972, 1977, Kleiner 1982; J. Belnap, *personal observation*), when it became dominant in many stands after a mild winter. Rimer (1998) conducted a preliminary study in this area quantifying the interaction between *Bromus* invasion and surface disturbance two years following the initial appearance of *Bromus*. Disturbed, non-invaded sites had significantly lower amounts of soil inorganic N than undisturbed, non-invaded sites during spring and this corresponded to a decrease in the size of the labile N pool. The introduction of *Bromus* lowered the size of the labile N pool and soil inorganic N in undisturbed sites to those observed in disturbed sites. In contrast, invasion had no effect on the size of the labile N pool and soil inorganic N in disturbed sites. Based on the initial results of Rimer (1998), we identified invaded and non-invaded stands of two community types within Virginia Park for more intensive study of the changes that occur in N cycling in undisturbed grassland ecosystems. The two community types were dominated by either *Hilaria jamesii* or *Stipa* spp. Three 30 × 20 m plots were established in both invaded and non-invaded stands of each community (12 total) during May 1996.

Litter biomass and chemistry

Standing and ground litter was collected during May 1996 within ten 0.25 × 0.25 m^2 quadrats randomly

located within each plot. All litter was removed and placed in paper bags. Subsamples of the standing litter of individual species were also collected for chemical analysis. The litter was weighed after oven drying at 70°C and all litter from within a plot was bulked for analysis. Litter C and N content were determined at the Central Analytical Laboratory at the University of Arkansas (Fayetteville, Arkansas, USA) using a CHN analyzer. Cellulose and lignin content were measured at the University of Wisconsin Soil and Forage Analysis Laboratory (Madison, Wisconsin, USA) using the forage fiber technique (Ryan et al. 1990). Mean values for each plot were used for statistical analysis, so n = 3 plots for each community type × invasion status category and n = 12 plots for the entire data set.

Potential microbial respiration and net N mineralization

Long-term soil incubations were performed to estimate potential microbial respiration and net N mineralization. Samples were collected from 10 randomly placed locations within each plot on 15 March 1997. Soils were collected using a polyvinyl chloride pipe 6 cm in diameter and 5 cm deep. Each core was placed in a soil tin and transported on ice to the laboratory. Soils from each plot were then bulked and passed through a 2-mm sieve, so n = 3 plots for each community type × invasion-status category and n = 12 plots for the entire data set. A subsample of each bulk sample was weighed, dried in an oven at 105°C for at least 48 h, and then reweighed to determine soil moisture.

A second subsample of each soil was placed back into the soil cores used for field collections. Glass filter paper was attached to the bottom of each core using rubber bands. The soil was incubated in a 1-L mason jar in a laboratory incubator set at 30°C. The sample rested on a layer of marbles because the bottom 5 mm of the jar was filled with deionized distilled water to prevent desiccation.

Samples were leached using no more than a 0.05 MPa vacuum on days 0, 2, 4, 9, 14, 19, 29, 59, 89, 142, 175, 209, 259, 338, and 415 using 150 mL of a nitrogen-free nutrient solution mixed using deionized-distilled water (Nadelhoffer 1990). Day 0 extracts were not used in the analysis, but served to remove inorganic N already in the soil. The NH_4^+ and NO_3^- within subsequent extractions were measured using an auto-analyzer (Alpkem Flow Solution 3000 [Alpken, College Station, Texas, USA]. Headspace samples were collected before and after leaching on each date with a 10-mL gas-tight syringe. CO_2 concentrations in the gas sample were measured using a LI-COR 6251 gas analyzer (LI-COR, Lincoln, Nebraska, USA) and analyzed using Sable Systems Software (Sable Systems International, Henderson, Nevada, USA). Net N mineralization is the change in total inorganic N content between sampling dates. Potential microbial respiration was calculated as the increase in CO_2 concentration between sampling dates.

Potential denitrification

Denitrification potential was measured using the denitrification enzyme activity (DEA) assay (Tiedje et al. 1989, Groffman et al. 1999). The DEA assay provides an index of the capacity for denitrification in a soil sample by optimizing O_2, NO_3^-, and C and inhibiting growth through the addition of chloramphenicol (Groffman et al. 1999). Ten grams of soil were placed into 100-mL gas-tight containers with 10 mL of media containing 0.72 g KNO_3/L, 0.50 g glucose/L, and 0.125 g chloramphenicol/L. The containers were sealed and made anaerobic by evacuating for 3 min under vacuum and then back flushing with N_2 gas. A 10% acetylene atmosphere was created by removing 10% of the headspace of each container with a syringe and replacing it with acetylene. The containers were then placed on an orbital shaker at 125 rpm. N_2O evolution was measured by taking gas samples (5 mL) at 30 and 90 min. The N_2O in the gas samples was analyzed using a gas chromatograph (Model GC-14 [Shimadzu, Plano, Texas, USA]) equipped with a 2-m Porpak Q column (Alltech, Deerfield, Illinois, USA) and an electron capture detector. Detector temperature was 300°C, column temperature 55°C, and the N_2 carrier flow rate was 30 mL/min. Mean values for each plot were used for statistical analysis, so n = 3 for each community type × invasion-status category and n = 12 for the entire data set.

Soil inorganic-nitrogen availability

Inorganic-N availability was measured in situ using ion-exchange resin bags (Binkley and Hart 1989, Lajtha 1988) beginning on 7 October 1996. Ion accumulation on resin bags depends on rates of N mineralization, ion form, water movement in the soil, and plant and microbial uptake (Binkley 1984, Binkley and Hart 1989). These are the same factors that determine the N availability for plants so resin bags provide a useful index of plant N availability (Binkley and Vitousek 1989, Fisher and Whitford 1995). Dowex MR3 mixed cation-anion resin (30 mL) (Sigma, Saint Louis, Missouri, USA) was sealed in nylon mesh bags and buried at 5 cm depth in the soil. Three bags were placed in each plot on each sampling date. Bags were extracted in 75 mL of 2 mol/L KCl within 24 h of collection and NH_4^+ and NO_3^- in the extract was analyzed on the auto-analyzer. Mean values for the three bags collected from each plot were used for all statistical analyses, so on each date n = 3 for each community type × invasion-status category and n = 12 for the entire data set.

Statistical analysis

All data were analyzed using the General Linear Models procedure of the SAS statistical package for

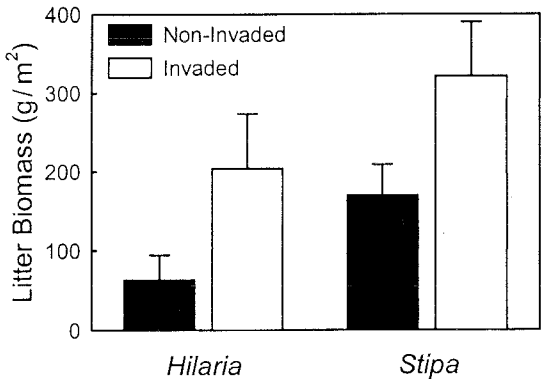

FIG. 1. Litter biomass for invaded and non-invaded *Hilaria jamesii* and *Stipa* spp. communities in Canyonlands National Park, Utah, USA. *Bromus tectorum* first appeared in Invaded sites in 1994. Litter collections were made during March 1996. Data are means and 1 SE. The statistical interaction between community and invasion was not significant. Community ($P = 0.0375$) and invasion ($P = 0.0217$) main effects were both significant.

Windows (SAS Institute 1991). Litter biomass, potential denitrification, and final values from long-term incubations were analyzed in a two-way (community × invasion status) factorial design. The interaction term for each test was not significant unless reported in the text. Inorganic N from resin bags and potential mineralization and microbial respiration from long-term incubations were analyzed using a repeated-measures ANOVA. The linearity of each regression model and the normality of the error terms were assessed using graphic analysis of residual terms following Neter et al. (1985). Data transformations were used when necessary to ensure that the data conformed to the assumptions of each statistical model. Mean values were compared using a Waller-Duncan multiple-range test. The mean value of all subsamples in a plot was used for all statistical analyses. A significance level of 0.05 was used for all statistical tests. All values are presented as the mean ± 1 SE.

RESULTS

Litter biomass and chemistry

Invasion significantly increased the amount of litter in *Hilaria* and *Stipa* communities (Fig. 1); mean litter biomass of plots with *Bromus* was over 125% greater than plots that were non-invaded. *Stipa* communities (245.7 ± 48.9 g/m²) also had significantly greater litter biomass than *Hilaria* communities (133.6 ± 46.4 g/m²). The lignin: N ratio of *Bromus* was significantly greater than that of *Stipa,* while values for *Hilaria* were not significantly different from the other species (Fig. 2A). The C:N ratio of *Bromus* was over 100% greater than *Hilaria,* and over 200% greater than *Stipa* spp. Differences in the lignin:N and C:N ratios were caused by *Bromus* litter having significantly lower ($P = 0.0058$) N content (3.1 ± 0.4 g/kg) compared to *Hilaria* (6.4 ± 1.2 g/kg) and *Stipa* (7.8 ± 1.0 g/kg). Carbon (410 ± 12 g/kg), cellulose (404 ± 23 g/kg), and lignin (42.9 ± 8.7 g/kg) content did not differ significantly ($P > 0.05$) among species.

Potential microbial respiration and net N mineralization

The cumulative amount of carbon respired did not differ significantly by community or invasion status (Fig. 3). The amount of C respired was almost 300 mg/kg in the first 50 d of the incubation, and this increased to ~400 mg/kg by day 415. All statistical interactions were not significant ($P > 0.05$) for net N mineralization, only the main effects of date ($P < 0.0001$) and invasion status ($P < 0.0001$) were significant. Higher rates of net N mineralization caused non-invaded sites to accumulative significantly more N than invaded sites for both communities (Fig. 4). The cumulative amount of N mineralized was significantly greater for sites without *Bromus* on each date after days 142 and 159 for the *Stipa* and *Hilaria* communities, respectively. Net nitrification contributed <15% of total N mineralized during the first 175 d of the incubation regardless

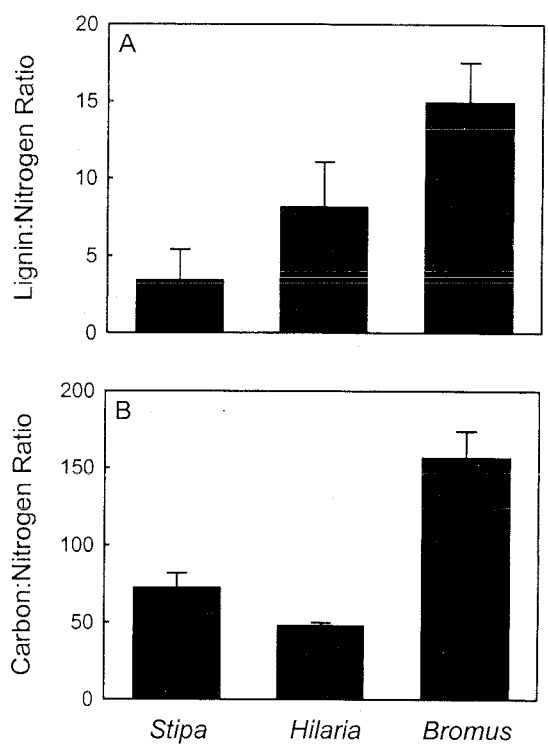

FIG. 2. (A) Lignin:N and (B) C:N ratios for litter of *Stipa* spp., *Hilaria jamesii*, and *Bromus tectorum* in Canyonlands National Park, Utah, USA. *Bromus tectorum* first appeared in Invaded sites in 1994. Litter collections were made during March 1996. Data are means and 1 SE. Differences were significant among species for lignin:N ($P = 0.0031$) and C:N ($P < 0.0001$) ratios.

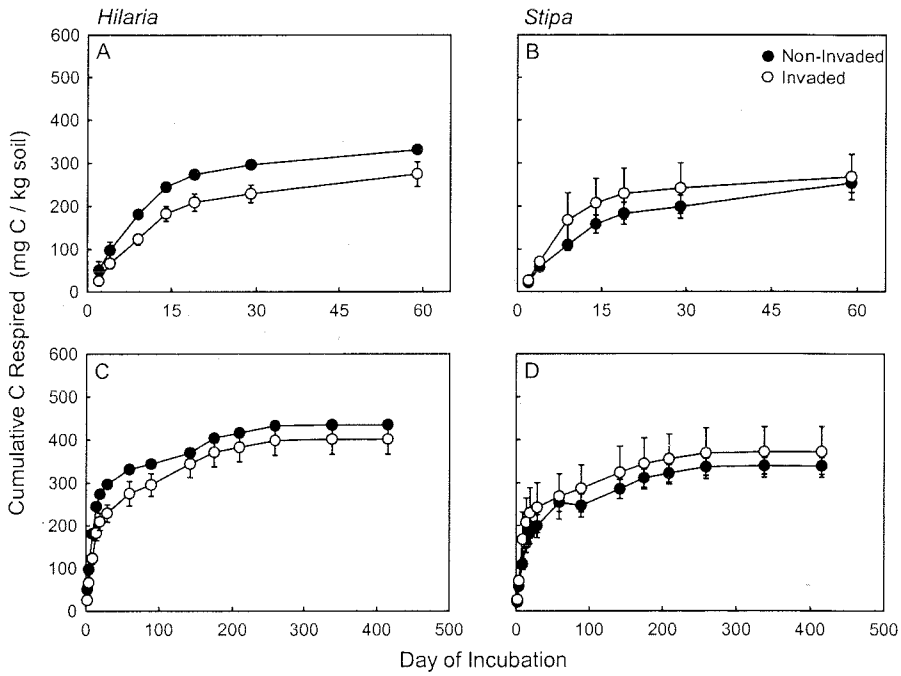

FIG. 3. Cumulative carbon respired during a 415-d laboratory incubation. (A) and (B) are for the first 60 d, while (C) and (D) are results for the entire incubation. Soils were collected from invaded and non-invaded *Hilaria jamesii* (A and C) and *Stipa* spp. (B and D) communities in Canyonlands National Park, Utah, USA. Data are means ± 1 SE. Only the main effect of date was significant ($P < 0.0001$); interaction terms and the main effects of invasion status and community were not significantly different.

of community type and invasion status. This increased to 30% by day 259 and 40% by day 338. No significant differences ($P > 0.05$) were detected between different treatments on each date.

The total cumulative amount of C respired during the incubation did not differ significantly between communities or by invasion status ($P > 0.05$) and the mean value was 383 ± 18 mg C/kg soil. In contrast, invasion caused a significant decrease ($P = 0.0024$) in the total amount of N mineralized. The mean value for non-invaded sites was 35.6 ± 5.8 mg N/kg soil compared to 17.6 ± 2.3 for invaded sites. The ratio of C respired to N mineralized has been used as an index of microbial immobilization (Schimel et al. 1985, Burke 1989, Holland et al. 1995, Frank and Groffman 1998*a*). Invasion caused a significant ($P = 0.0017$) increase in the immobilization index, from 11.4 ± 1.4 in non-invaded sites to 23.6 ± 3.3 in invaded sites (Fig. 5).

Potential denitrification

Invasion caused a significant ($P = 0.0446$) decrease in denitrification enzyme assay (DEA) activity (Fig. 6). Fluxes for invaded communities (45.7 ± 12.0 μg N_2O-$N \cdot kg^{-1} \cdot h^{-1}$) were only 32% of those observed in non-invaded communities (144.8 ± 38.0 μg N_2O-$N \cdot kg^{-1} \cdot h^{-1}$). DEA activity did not differ significantly among communities.

Soil inorganic N availability

Soil inorganic N availability exhibited significant seasonal variation in both community types regardless of invasion status (Fig. 7). Values for the *Hilaria* sites were greatest during late spring, while values for *Stipa* were greatest during late summer and spring. Differences in inorganic N between invaded and non-invaded communities were not significantly different on any date, except during late spring of 1997 in *Hilaria* sites where invasion caused a 50% decrease in inorganic N. Comparisons for the *Stipa* sites are not possible on this date because rodent activity disturbed ion-exchange resin bags in invaded sites.

Variation in total inorganic N in resin bags was due to changes in ammonium; nitrate did not vary significantly ($P = 0.2209$) by date, community, or invasion status and the mean value was 0.5 ± 0.1 μg NO_3-$N \cdot bag^{-1} \cdot d^{-1}$. Ammonium: nitrate ratios in resin bags were typically greater than 2:1 and could be greater than 10:1 during peaks in inorganic-N availability. Actual ratios are likely to be much greater than this because nitrate mobility can be 30-fold greater than that of ammonium (Binkley 1984).

DISCUSSION

Bromus has displaced much of the native vegetation and become the dominant species in North American

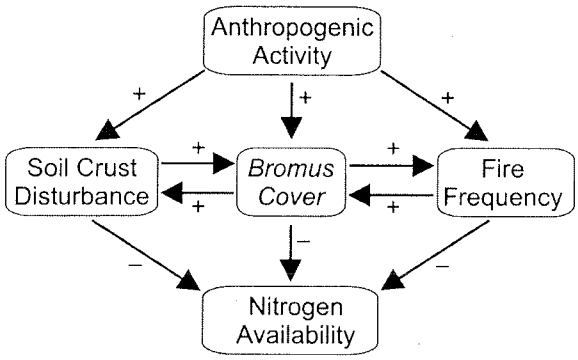

FIG. 9. Hypothesized relationships among anthropogenic activity, soil crust disturbance, *Bromus* cover, fire frequency, and plant N availability. Arrows with "+" signify a positive influence; arrows with "−" signify a negative influence.

of N transformations by altering small fractions of soil organic matter. Wedin and Tilman (1990) observed large changes in net N mineralization only three years after planting monocultures of five different grass species. The divergence among species was caused by changes in the size of the labile N pool within the soil (Wedin and Pastor 1993). Rimer (1998) observed a similar pattern for *Bromus* two years following invasion. The size of the labile N pool was 50% lower in invaded sites, causing corresponding decreases in net N mineralization and inorganic-N availability. Bolton et al. (1990) also observed that net mineralization was lower in sites dominated by *Bromus* than in neighboring sites with native grasses.

Rates of N transformation and loss are rapid in arid ecosystems (Peterjohn and Schlesinger 1990, Schlesinger et al. 1990); Peterjohn and Schlesinger (1990) estimate that 77% of all N input is subsequently lost to the atmosphere. *Bromus* invasion may cause a short-term decrease in rates of N loss by decreasing inorganic-N availability and denitrification enzyme activity. Denitrification enzyme activity integrates the longer-term factors that control denitrification (Groffman and Tiedje 1989, Tiedje et al. 1989, Groffman et al. 1999), and correlates well with indices of C and N availability in arid ecosystems (Peterjohn 1991). However, one of the long-term consequences of *Bromus* invasion is an increase in fire frequency (Klemmedson and Smith 1964, Whisenant 1992). Sites dominated by *Bromus* are 10 to 500 times more likely to burn than sites with native species (Knapp 1996), and *Bromus* invasion can decrease the fire interval from >100 yr to <5 yr (Whisenant 1992). Loss of N during fire can be significant in grassland ecosystems (Vitousek and Howarth 1991, Turner et al. 1997). Large decreases in total and inorganic N are observed following fire in sites dominated by *Bromus* (Blank et al. 1994, Halvorson et al. 1997), so while *Bromus* invasion may initially conserve N within the ecosystem by promoting N immobilization and decreasing gaseous N loss, the long-term consequence may be greater N loss due to volatilization during fire.

Bromus invasion and surface disturbance caused by land-use change have established positive feedbacks among *Bromus* cover, fire frequency, and disturbance of the biological soil crust that, in conjunction, will decrease N availability (Fig. 9). The decrease in inorganic N suggests that *Bromus* can decrease resource availability only two years following establishment by altering litter biomass and chemistry. Nitrogen availability will be decreased further in the longer term because of the increase in fire frequency and volatile loss of N during fires (Halvorson et al. 1997). The increase in fire frequency also favors *Bromus,* because it eliminates competition from native perennial species that cannot survive fire (Whisenant 1992, Brandt and Rickard 1994, Knapp 1996). N_2-fixation by the biological soil crust is the dominant source of N input into many arid ecosystems (West and Skujins 1977, Evans and Ehleringer 1993, Evans and Johansen 1999). Surface disturbance caused by land-use change has eliminated the biological soil crust, decreasing soil N content, net N mineralization, and inorganic-N availability (Evans and Ehleringer 1993, 1994, Evans and Belnap 1999). The introduction of *Bromus* will facilitate degradation of the biological soil crust and the decrease in N availability because the dominant organisms within the crust are photosynthetic (Lange 2001) and the increase in plant cover with *Bromus* invasion causes large decreases in light availability at the soil surface. The decrease in N availability caused by the positive feedbacks among disturbance of the biological soil crust, *Bromus,* and fire frequency could have important consequences for the stability of these arid ecosystems, causing directional changes in resource availability and species composition that may be irreversible.

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