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Authors: Parker, Sophie S., and Schimel, Joshua P.

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Invasive Grasses Increase Nitrogen Availability in California Grassland Soils

Sophie S. Parker and Joshua P. Schimel*

As Europeans colonized California, they introduced annual grasses from the Mediterranean Basin. These exotic annual grasses eventually invaded grasslands throughout the state, some of which were once dominated by native perennial grass species. Annual grasses differ from perennials in their phenology, longevity, rooting depth, litter chemistry, and interaction with the microbial community. As these traits may influence plant nitrogen (N) use, it is likely that the invasion by annual species resulted in changes in the availability and cycling of N in California grassland systems. We addressed the question of how invasive annual grasses influence rates of N cycling by measuring N pool sizes and rates of net and gross mineralization and nitrification, gross immobilization, and the denitrification potential of soils from experimentally planted annual and perennial-dominated grasslands. With an increase in annual grass cover, we saw increases in ammonium (NH_4^+) pool sizes and rates of N mineralization, nitrification, and denitrification in soils. These differences in N status suggest that N cycling in California grasslands was altered at sites where native perennial bunchgrasses were invaded by nonnative annual grasses. One consequence of annual grass invasion may be a legacy of NH_4^+-enriched soils that hinder the reestablishment of native perennial grass species.

Key words: Functional group, invasive species, nitrogen mineralization.

Plant invasions can change ecosystems with regard to biodiversity, productivity, species composition, and nitrogen (N) retention by altering the availability of N for plant growth (Evans et al. 2001). N alterations resulting from plant invasions are well documented (see reviews: Corbin and D'Antonio 2004b, Ehrenfeld 2003, Liao et al. 2007) and include examples from around the world. Plant invasion can alter soil N cycling by changing the nutrient content of plant litter (Rothstein et al. 2004), by altering the rate of N uptake or loss from the soil (Windham and Ehrenfeld 2003; D'Antonio and Hobbie 2005), or by changing the microbial processing of N (Hawkes et al. 2005; Wolfe and Klironomos 2005).

European settlement of California resulted in a dramatic shift in grassland plant species composition with the invasion of nonnative annual grasses from the Mediterranean Basin (Bartolome et al. 1986; Jackson 1985; Mooney et al. 1986). N is an important limiting nutrient in California grasslands (George et al. 1985), and low N availability can limit the growth of grasses even in dry years (Jones and Woodmansee 1979). Given the importance of N in California grassland systems, the vast change in species composition that occurred with invasion begs the question: How has grassland N cycling responded to the invasion of nonnative annual grass species?

Although it is impossible to roll back the clock and replay the historic invasion of California grasslands to determine whether the N status of soils shifted, we can glean useful information from present-day experimental comparisons of the differing effects of exotic vs. native grassland plants on soil N cycling. The historical dominance of purple needlegrass [*Nassella pulchra* (Hitchc.) Barkworth] and other native bunchgrasses is a good assumption for many grasslands throughout the state, including areas of the coast range that receive moist coastal air (D'Antonio et al. 2007). Historically, our study site is thought to have been dominated by perennial grassland, and results from our study may be extrapolated to the many invaded grasslands of perennial bunchgrass in California (e.g., Burcham 1957; Heady 1977). At sites such as these, comparing the effects of native perennial grasses to those of exotic annual grasses can provide us with information regarding the possible past effects of annual grass invasion.

Invasive annual grasses differ from native perennial grasses in several ways that could lead to differences in N

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* Graduate Student and Professor, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106. Current address of first author: Ecoregional Ecologist, The Nature Conservancy, 523 W. Sixth St., Suite 1216, Los Angeles, CA 90014. Corresponding author's E-mail: sophie_parker@tnc.org

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Interpretive Summary

Invasive species tend to thrive under high-nutrient conditions. In California grasslands, fertile soils high in nitrogen (N) have been found to promote the growth of invasive annual grasses. Unfortunately, it is difficult to discern in the field whether invasive species are causing the high soil N conditions or just responding to them by being more successful and, therefore, becoming more abundant than natives when N is plentiful. To test how different grass types influence their soil environment with regard to N, we used experimental plantings of annual and perennial grasses on tilled, homogenized, California grassland soils. We found that as annual grass cover increased, soil ammonium (NH_4^+) pools and some rates of N cycling increased. These findings provide a piece of the puzzle as to how California grassland ecosystems may have changed when annual grasses became dominant. The differences in N status between the two soil types suggest that with the historic invasion of annual grasses, N availability in California grassland soils increased. The legacy of the annual grass invasion may be relatively N-rich soils that favor more weedy invasive annual grass species. These species require more N for growth than native perennials, and they would, therefore, be promoted when soil N availability is high. The lush growth of annual grasses under high N conditions may hinder the reestablishment of more slow-growing, N-conserving, native perennial grass species. Therefore, attempts to restore native perennial grasses in California grasslands may be more successful if they take place on low-N soils or with planned soil amendments that decrease N availability to plants.

cycling in soils associated with each grass type. In contrast to perennial bunchgrasses, which grow with space between individuals, annuals form a dense, homogenous carpet across the landscape. This could have produced differences in the spatial patterns of N use and cycling (Parker 2006). Although annuals produce shallow roots that typically do not grow deeper than 50 cm (Holmes and Rice 1996), perennials have much deeper root systems (Jackson et al. 1988). Shallow rooting by annuals results in less-effective water uptake at deeper depths in the soil (Seabloom et al. 2003) and could contribute to differences in N uptake as well. Annuals and perennials also differ in their life history traits and phenology. Annual seeds germinate after the first rains in the fall and grow during the winter and early spring. By the time rainfall tapers off in late spring, annuals have set seed and senesced. In contrast, perennial roots, which are already in place in the fall, break dormancy and begin to elongate and take up water, and perhaps N, with the first rains (Holmes and Rice 1996). Because they have access to deeper sources of water, perennials are able to maintain activity later into the summer and may have access to N later in the season. Given the large differences between annual and perennial grasses in aboveground growth form and phenology and belowground root growth and resource use, they are likely to produce substantially different patterns and rates of N cycling in soils (Chapin et al. 1994; Vitousek 1990). If this is true, then the invasion of annuals into native, perennial-dominated grasslands likely changed N cycling patterns in California grasslands.

In this study, we ask: How do native perennial and invasive annual grasses influence rates of N cycling in California grassland soils? To answer this question, we measured N pool sizes and rates of net and gross mineralization and nitrification and assessed the denitrification potential of soils from grasslands that were experimentally planted with annual and perennial grass species.

Materials and Methods

Site Description. The study was conducted at the University of California Sedgwick Reserve, in the Santa Ynez Valley (43°42′30″N, 120°2′30″W). The reserve is located in the foothills of the San Rafael Mountains. Its grasslands are currently dominated by nonnative, annual grass species, but notable relict stands of native, perennial bunchgrasses exist in multiple locations throughout the reserve. The climate is Mediterranean, with hot, dry summers (high temperatures in the mid 30s C) and mild winters where temperatures rarely dip below freezing (Nahal 1981). Rainfall begins in the autumn and is delivered in distinct events through the winter and spring, ceasing entirely during the summer months. Average rainfall is 380 mm/yr, but annual precipitation totals vary greatly, totaling more than 600 mm in some years and less than 200 mm in others. Coastal fog is common during the warmer months of the year. Given the climate and topography and the presence of remnant stands of native perennial bunchgrasses, perennial bunchgrass species are likely to have been dominant members of the grassland community on the reserve before the invasion of nonnative annual grasses.

All soils were collected from experimental plots that were established in the Figueroa Creek drainage area of Sedgwick Reserve (Seabloom et al. 2003). The soils at the site are Argixerolls, with nearly flat (less than 2%) slopes. In the fall of 1998, a 2.5-ha field was tilled and disked, yielding fairly uniform soils. Eight plots measuring 3 by 3 m were seeded at a density of 500 live seeds/m^2. This seeding rate eliminated seed limitation by ensuring that few microsites remained unoccupied after the first season of growth (Seabloom et al. 2003). Four plots were seeded with a mix of three native perennial grasses—California brome (*Bromus carinatus* Hook. & Arn.), blue wildrye (*Elymus glaucus* Buckley), and *Nassella pulchra*—and four other plots were seeded with three nonnative annual grasses—soft brome (*Bromus hordeaceus* L.), foxtail brome (*Bromus madritensis* L.), and mouse barley (*Hordeum murinum* L.). Natural cross-invasion occurred between seeding in 1998 and the beginning of the soil sampling in 2003, resulting in grass plots with a range of

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annual and perennial cover. Percentage of cover estimates were made in the spring of 2003. These visual estimates were made in a designated 0.5 by 0.5-m subplot where soil sampling was to be conducted within each of the larger 3 by 3-m plots. These cover estimates, when compared with yearly measurements of clipped, aboveground biomass from a separate area within each 3 by 3-m plot designated for sequential, destructive harvests, were found to be a good proxy for grass biomass during the study period (E. W. Seabloom, unpublished data).

Soil Collection and Analysis. Soils were collected 10 times during the course of a 22-mo period beginning in December 2003. This period included precipitation events during the 2003 to 2004 and 2004 to 2005 rainfall years. We collected at least one soil core in each season to provide a good representation of soil N status across seasons. On each sampling date, a corer measuring 10 cm deep and 2.5 cm in diameter[1] was used to collect one soil core from the same designated 0.5 by 0.5-m subplot where cover estimates were done within each of the eight 3 by 3-m plots. Sites for coring within plots were chosen at random with the exception of plots with uneven plant cover, where coring took place within 5 cm of the base of the nearest randomly selected plant. Soils were sieved to 4 mm, and rocks and roots were removed. Soils were then stored at 4 C for no longer than 4 wk before analysis.

Gravimetric soil moisture was calculated by measuring the mass of soils before and after drying at 80 C for 48 h. We estimated 100% water holding capacity (WHC) for each soil sample by measuring the gravimetric water content of soil that was saturated and allowed to drain more than 2 h in a covered filter funnel. Allowing soils to sit for longer than 2 h did not result in significantly more drainage, so 2 h was deemed sufficient for the measurement of WHC in soils from our site. Dissolved inorganic N (DIN) was extracted from 10-g soil subsamples using 40 ml of 0.5 M K_2SO_4. Samples were filtered before freezing and subsequent flow-injection analysis on a Lachat auto-analyzer.[2] Ammonium (NH_4^+) was analyzed by a diffusion method (Lachat method 31-107-06-5-A, Milwaukee, WI), and nitrate (NO_3^-,) was analyzed using Griess-Ilovsay reaction after Cd reduction (Lachat method 12-107-04-1-B, Milwaukee, WI).

Net N mineralization and nitrification were quantified using in situ intact core incubations of paired soil samples following a procedure similar to that developed by DiStefano and Gholz (1986). An ''initial'' core was taken for the immediate analysis of NH_4^+ and NO_3^-, and a ''final''14 core was collected and returned to the ground for a 1-mo incubation. Incubating soil cores were encased in polyvinyl chloride tubes and capped on top and bottom with resin ''cookies'' to isolate the core from the surrounding soil and to capture any vertical movement of DIN into or out of the core. Each cookie consisted of a 1.5-cm-tall ring of 2.5-cm-diam vinyl tubing filled with 5 g of exchangeable anion/cation resin[3] contained in a nylon stocking sealed with a plastic cable tie. The rate of net N mineralization was calculated as the final concentration of DIN in the soil core and the bottom resin cookie minus the concentration of DIN in the initial soil core. The top resin cookie was used to capture incoming N, which was excluded from the calculation of N mineralization. Net nitrification rates were determined by considering NO_3^- concentrations alone.

We used the ^{15}N pool dilution technique to estimate gross rates of mineralization and nitrification in sieved soils from the following collection dates: November 24, 2004; February 17, 2005; and April 14, 2005. Separate soil samples were used for $^{15}NH_4^+$ and $^{15}NO_3^-$ additions; each sample contained a dry weight equivalent of 12.75 g of soil adjusted to 50% of WHC. We used 99% enriched $(^{15}NH_4)_2SO_4$ and $K^{15}NO_3$ to create ^{15}N-labeled solutions of 25.5 mg ^{15}N/L. Using a syringe and needle, we dispensed 0.5 ml of solution as evenly as possible through each soil sample; this constituted an addition of 1-μg N/g of dry soil. T_0 samples were extracted in 40 ml of 0.5 M K_2SO_4 after 15 min. T_{final} samples were extracted after a 24 h incubation at 20 C. Before isotopic analysis of ^{15}N, samples were analyzed for $^{14}NH_4^+$ and $^{14}NO_3^-$. Those samples containing less than 1 mg/L of N were supplemented with a known amount of N (0.5 ml of 100 [ppmw] NH_4^+) to provide for sufficient N for detection during analysis. All samples were filtered through glass-fiber filters into 50-ml specimen cups, and 0.2 g of MgO was added to raise the pH of solutions and diffuse NH_4^+. The gross production of NH_4^+ was measured from the samples to which $^{15}NH_4^+$ had been added. NH_3 vapor was captured from these samples during the course of 7 d in sealed specimen cups using acidified, glass-fiber, filter-disk traps sealed between two strips of Teflon (polytetrafluoroethylene [PTFE]) tape. Samples that were enriched with $^{15}NO_3^-$ were left loosely capped for 3 d after the addition of MgO to allow NH_3 to escape, and then 0.4 g of Devarda's alloy was added to reduce NO_3^- to NH_4^+ (Brooks et al. 1989). Gross NO_3^- production was then measured by capturing NH_3 vapor during the course of 7 d on filter-disk traps. Once diffusions were complete, the tape was removed from the traps, and disks were packaged in tin weigh boats and shipped to the ^{15}N Analysis Service, Department of Natural Resources and Environmental Sciences at the University of Illinois (Urbana, IL) for analysis of $^{15}NH_4^+$ and $^{15}NO_3^-$ by mass spectroscopy. The isotope dilution model of Kirkham and Bartholomew (1954) was used to calculate rates of gross mineralization and nitrification.

Potential rates of denitrification were measured using a short-term anaerobic assay developed by Tiedje et al.

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(1989). Our assay was conducted using 10 g of fresh soil in air-tight, 50-ml tubes with butyl rubber septa. A 10-ml aliquot of solution containing 0.1 mg NO_3^- − N, 0.04 mg dextrose, and 0.01 mg chloramphenicol per gram was added to the soil, and the tubes were capped and flushed with helium for 10 min to create an anaerobic environment. We blocked the production of N_2 using acetylene gas and measured resulting N_2O using gas chromatography. Denitrification potentials were calculated as a function of the N_2O gas produced during the course of the 3-h incubation.

Statistical Analyses. We tested the effect of the percentage of annual grass cover on the following response variables: NH_4^+ and NO_3^- pool sizes, net and gross rates of N mineralization and nitrification, gross rates of NH_4^+ and NO_3^- immobilization, and rates of potential denitrification using linear regressions. To meet the assumption of linear regression analysis that the independent variable be a measurement rather than a nominal value, the percentage of annual cover values were arcsin-converted before analysis.

Previous work in these grasslands demonstrated that significant differences exist in N cycling dynamics between the summer and the growing season (Parker 2006). Therefore, we approached our data set with this two-phase, rainfall-driven, seasonal periodicity of the study system in mind and first categorized all samples as either summer (roughly May to October) or growing season (roughly November to April), depending on the time of year that they were collected. The summer samples included soils from summer 2004 (May 5, 2004, and September 1, 2004) and summer 2005 (July 6, 2005; August 5, 2005; and September 4, 2005); all were collected after grass senescence, before the first autumn rains, and had a gravimetric soil moisture content of less than 10%. Samples collected during the growing season, when soils were moist and grasses were actively growing, included those from growing season of 2003 to 2004 (December 19, 2003, and March 13, 2004), and those from growing season of 2004 to 2005 (November 24, 2004; February 17, 2005; and April 14, 2005). This grouping scheme results in five samples from the summer and five from the growing season. Taking the mean of each of these groups of five values gave us seasonal (summer season vs. growing season) means. We then found the overall mean for the response variables by taking the average of these seasonal means. This approach gives a representative value that incorporates both seasonal differences and interannual variability during the sampling period.

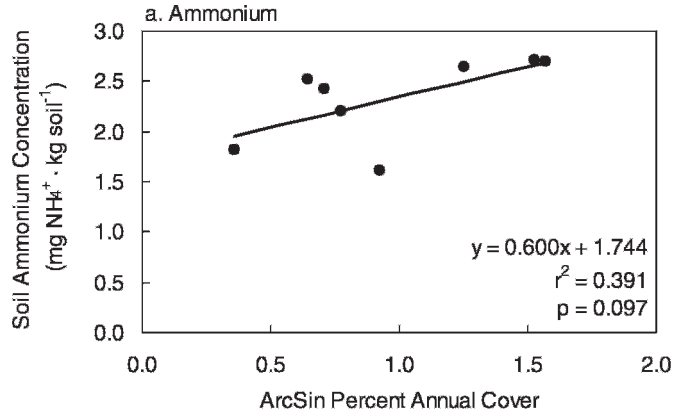
Before linear regression and correlation analysis to produce r^2 and P statistics, the data were tested for normality and homogeneity of variance using histograms, normal probability plots, plots of residuals vs. predicted values, and by reviewing skewness and kurtosis statistics. Data that did not pass the assumptions tests were log-transformed before analysis. Gross rates of N mineralization, nitrification, and immobilization were determined only in soils collected during the 2004 to 2005 growing season, so our results reflect means from only one growing season for these gross process rates. All statistics were performed using SYSTAT 10 (Systat 2000).

Although a cutoff point of $P \leq 0.05$ is frequently used to characterize statistical significance, this value is an arbitrary boundary with potentially little ecological meaning. Given the inherent heterogeneity of soils, the collection a large and logistically unfeasible number of replicates may be required to obtain values $P > 0.05$ from statistical tests when conducting soil microbial research (Klironomos et al. 1999). Hereafter, we refer to results with a $P \leq 0.05$ as *significant*, and those with a $P > 0.05$ but ≤ 0.1 as *marginally significant*. Given the limited sample size used in our tests, rejecting test results of $P > 0.05$ but ≤ 0.1 as *not significant* raises the likelihood of a Type II error, where a real relationship in the data could be mistakenly classified as insignificant and wrongly rejected.

Results and Discussion

Several measures of soil N availability and N cycling increased as annual grass cover increased. There was a positive linear relationship between percentage of annual cover and soil NH_4^+ (Figure 1). The correlation between percentage of annual cover and soil NH_4^+ was marginally significant ($r^2 = 0.391$, $P = 0.097$), whereas the positive linear relationship between annual cover and soil NO_3^- was not statistically significant ($r^2 = 0.191$, $P = 0.278$). Net rates of N cycling increased with the percentage of annual cover (Figure 2). The linear regression of net N mineralization on the percentage of annual cover was marginally significant at ($r^2 = 0.392$, $P = 0.097$), and there was a strong, statistically significant, positive correlation between net nitrification and the percentage of annual cover ($r^2 = 0.764$, $P = 0.005$). The positive correlation between the percentage of annual cover and the potential denitrification was also marginally significant ($r^2 = 0.473$, $P = 0.059$; Figure 3). The linear relationships between the percentage of annual cover and the gross NH_4^+ mineralization ($r^2 = 0.104$, $P = 0.435$), gross NH_4^+ immobilization ($r^2 = 0.168$, $P = 0.312$), gross nitrification ($r^2 = 0.079$, $P = 0.497$), and gross NO_3^- immobilization ($r^2 = 0.147$, $P = 0.347$) all had positive slopes, but these relationships were not statistically significant. The lack of statistical significance in many of the positive linear relationships and the marginal significance of others may be due in part to the range of the percentage of annual cover used in our experimental plots. All but one of the plots ranged from 60 to 100% annual grass cover. This artifact of differential grass growth rates in the experimental plots may have

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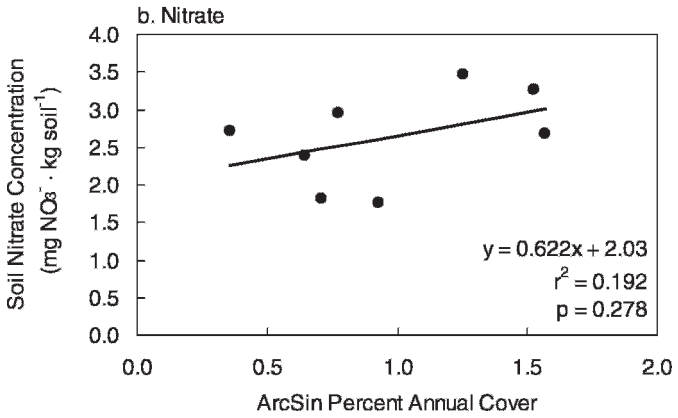
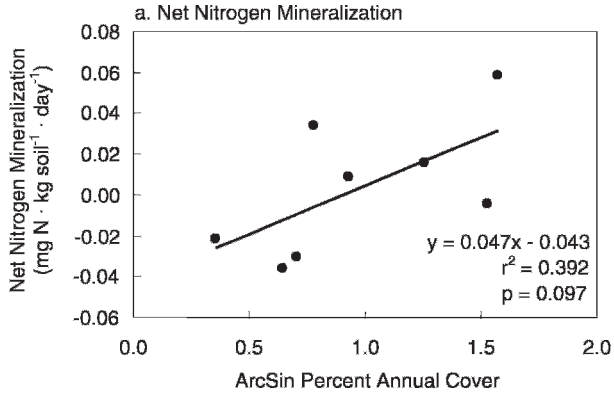


Figure 1. The effect of annual cover on (a) ammonium and (b) nitrate concentrations in soils at Sedgwick Reserve. Data points represent overall mean values for soil N status in each of the eight plots. These overall means were calculated by taking the average of summer vs. growing season means derived from samples taken over a 22-mo period from each plot. Summer means were derived from samples collected during the summer months: May 5, 2004; September 1, 2004; July 6, 2005; August 5, 2005; and September 4, 2005. Growing season means were calculated using samples taken on December 19, 2003; March 13, 2004; November 24, 2004; February 17, 2005; and April 14, 2005.



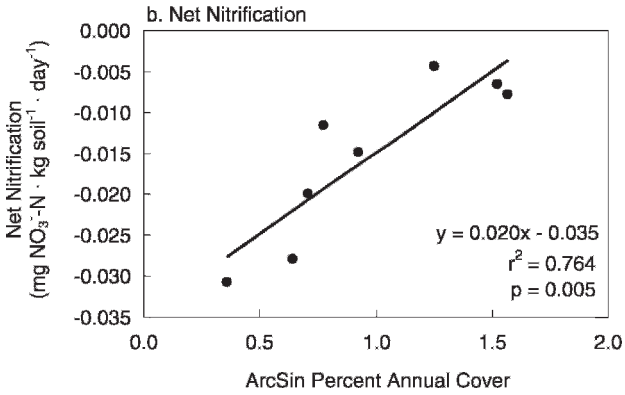


Figure 2. The effect of annual cover on net rates of (a) mineralization and (b) nitrification in soils at Sedgwick Reserve. Data points represent overall mean values for soil N status in each of the eight plots. These overall means were calculated by taking the average of summer vs. growing season means derived from samples taken during a 22-mo period from each plot. Summer means were derived from samples collected during the summer months: May 5, 2004; September 1, 2004; July 6, 2005; August 5, 2005; and September 4, 2005. Growing season means were calculated using samples taken on December 19, 2003; March 13, 2004; November 24, 2004; February 17, 2005; and April 14, 2005.

limited our ability to test statistically for differences between annual-dominated and truly perennial-dominated systems.

Because this experiment used seeded plots, rather than relict stands, the increases in NH_4^+ pool sizes and some N cycling rates with increasing annual cover are likely due to the influence of the plants on soil processes during the 4 yr after seeding. Several mechanisms can be evoked to explain these changes in soil N availability and process rates. Different plant species can affect N dynamics through their differences in growth form, life history, aboveground and belowground plant structures, tissue chemistry, physiology, and interactions with soil microbes (Ehrenfeld 2003). Although some of the relationships we observed between annual cover and N pools or process rates were relatively weak (some were only marginally significant at $P \leq 0.1$, and others were not statistically significant at all), it is likely that the relationships would grow stronger over time as either annuals or perennials remain in place and reinforce their unique influence on soil properties. Annual and perennial grasses have been found to promote differences in both soil water availability through water uptake (Holmes and Rice 1996; Hull and Muller 1977) and soil N status through N uptake (Aanderud and Bledsoe 2009), both of which could

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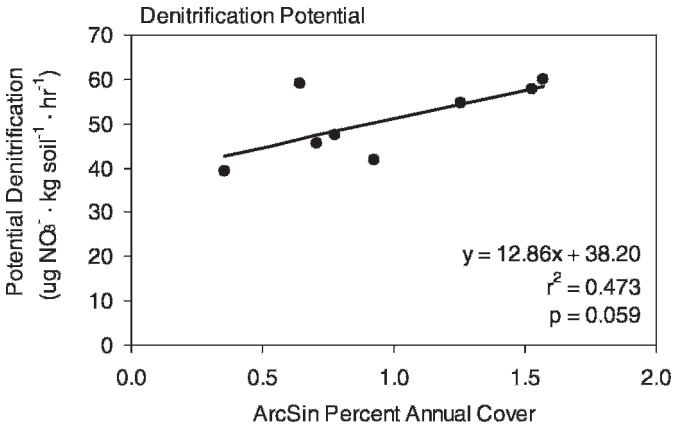


Figure 3. The effect of annual cover on rates of potential denitrification in soils at Sedgwick Reserve. Data points represent overall mean values for soil N status in each of the eight plots. These overall means were calculated by taking the average of summer vs. growing season means derived from samples taken over a 22-mo period from each plot. Summer means were derived from samples collected during the summer months: May 5, 2004; September 1, 2004; July 6, 2005; August 5, 2005; and September 4, 2005. Growing season means were calculated using samples taken on December 19, 2003; March 13, 2004; November 24, 2004; February 17, 2005; and April 14, 2005.

lead to differentiation in the soils of annual grass-dominated vs. perennial grass-dominated systems over time.

Concentrations of NH_4^+ and rates of N mineralization, nitrification, and denitrification increased with increasing annual grass cover. This may be due in part to differences in size and growth form between the annual and perennial grasses present in this system. Perennial bunchgrass individuals are much larger and more deeply rooted than annuals (Holmes and Rice 1996; Jackson et al. 1988)—they likely support a larger microbial community through increased root exudation and litter inputs (Bokhari 1977; West and Donovan 2004), which stimulate microbial growth (Clarholm 1985). Microbial biomass and soil respiration rates are higher immediately underneath perennial bunchgrass individuals than under adjacent annual grasses (Parker 2006). This could lead to increased microbial demand for N and explain the corresponding decrease in NH_4^+ observed under perennial grasses.

Higher NH_4^+ pools with increasing annual cover may also be due to differences in phenology between annual and perennial grasses. Annuals set seed and senesce earlier in the spring than deeply rooted perennials, which can access deeper soil water resources and live longer into the summer months (Jackson and Roy 1986; Holmes and Rice 1996; Major 1988). We found the positive effect of annual cover on NH_4^+ pool sizes was strongest during the summer (data not shown), likely because annual plant uptake would not occur during this time.

Higher concentrations of NH_4^+ in annual-dominated soils allow for higher rates of nitrification. The strong correlation we found between the percentage of annual cover and the net nitrification corresponds well with what has been found in studies examining the differential effects of native and exotic grass monocultures on gross rates of nitrification in soils (Hawkes et al. 2005). This is in contrast to perennial-dominated soils where the exudate- and litter-rich rhizosphere of perennial roots (Bokhari 1977; West and Donovan 2004) may selectively promote the growth of heterotrophic microbes, which outcompete nitrifying bacteria for NH_4^+ (Kindaichi et al. 2004), reducing nitrification when perennials dominate. Increased nitrification would cause high NO_3^- availability under annuals, leading to higher rates of denitrification. This may contribute to the higher denitrification potentials we observed with increasing annual cover.

Over many years, the differences in physiology and life-history traits that distinguish long-lived perennials from annuals would select for higher annual cover under conditions of high NH_4^+ availability, mineralization, nitrification, and denitrification. Annuals are unable to store N in their tissues from one year to the next and must rely on N from litter, soils, and dead seedlings when they grow from seed each fall (Eviner and Firestone 2007). In contrast, perennial grasses can survive for dozens to possibly hundreds of years (Hamilton 1997) and may translocate N from their senescing shoots to their long-lived roots at the end of the growing season, allowing them to survive in soils with low NH_4^+ availability (Woodman-see and Duncan 1980) or where N cycling rates are slow. In addition, previous work at the site demonstrated that perennial-dominated plots lose more N through leaching than annual-dominated plots (Parker 2006), suggesting that differences in leaching rates and N use would eventually leave annual grasslands relatively enriched in N in comparison to perennial grasslands. Because annual-dominated plots have higher soil N yet lose less N to leaching, the distinct seasonal changes in the physiology of annual grass may contribute to the retention of N in the system. It is possible that annuals may leave N in the soil during the summer when water is not there to allow plants to take it up. Both previous investigations at this site (Parker 2006) and Jackson et al. (1988) showed that in annual grasslands, N accumulates in soils during the course of the summer. Once the rains return and the growing season begins in the fall, the uptake of N by rapidly growing annual grasses and higher rates of denitrification under wet conditions may lead to the loss of N. This may leave less soil N to be leached from annual-dominated systems.

In conclusion, we have evidence that NH_4^+ availability and some N process rates increase with annual grass cover. Our findings support the idea that the invasion of annual grasses into perennial-dominated systems resulted in

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changes in N cycling in California grasslands that likely benefited the weedy invaders. The likely shift with invasion toward increased NH_4^+ availability and higher rates of N mineralization favors annual grass species that have faster relative growth rates and require more N for growth (Grime and Hunt 1975). Enhanced soil N can lead to increased growth of exotic annual grasses (Maron and Connors 1996; Brown et al. 2000), and this increased growth may prevent the reestablishment of perennial grasses, which are slower-growing and more N-conserving (Claassen and Marler 1998). Studies have shown that N fertilization has no effect on the productivity of native perennial grasses (Abraham et al. 2009), and that amending grassland soils with carbon can reduce rates of N mineralization and nitrification and decrease the degree to which exotic annuals competitively suppress the seedlings of native perennial bunchgrasses over the short term (Corbin and D'Antonio 2004a). Therefore, attempts to restore native perennial grasses in California grasslands may be more successful on low-N soils.

Sources of Materials

[1] Core Sampler, AMS Inc., American Falls, ID 83211-1230.

[2] Lachat Instruments Automated Ion Analyzer, QuikChem 8500 Series 2 FIA System, Hach Company. Loveland, CO 80538-8842.

[3] Mixed-bed exchange resin IO NAC-NM60, Mallinckrodt Baker, Inc., Phillipsburg, NJ 08865.

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