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Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework?

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Abstract. Theoretical and empirical work has established a positive relationship between resource availability and habitat invasibility. For nonnative invasive annual grasses, similar to other invasive species, invader success has been tied most often to increased nitrogen (N) availability. These observations have led to the logical assumption that managing soils for low N availability will facilitate restoration of invasive plant-dominated systems. Although invasive annual grasses pose a serious threat to a number of perennial-dominated ecosystems worldwide, there has been no quantitative synthesis evaluating the degree to which soil N management may facilitate restoration efforts. We used meta-analysis to evaluate the degree to which soil N management impacts growth and competitive ability of annual and perennial grass seedlings. We then link our analysis to current theories of plant ecological strategies and community assembly to improve our ability to understand how soil N management may be used to restore annual grass-dominated communities. Across studies, annual grasses maintained higher growth rates and greater biomass and tiller production than perennials under low and high N availability. We found no evidence that lowering N availability fundamentally alters competitive interactions between annual and perennial grass seedlings. Competitive effects of annual neighbors on perennial targets were similar under low and high N availability. Moreover, in most cases perennials grown under competition in high-N soils produced more biomass than perennials grown under competition in low-N soils. While these findings counter current restoration and soil N management assumptions, these results are consistent with current plant ecological strategy and community assembly theory. Based on our results and these theories we argue that, in restoration scenarios in which the native plant community is being reassembled from seed, soil N management will have no direct positive effect on native plant establishment unless invasive plant propagule pools and priority effects are controlled the first growing season.

Key words: annual grasses; carbon addition; cheatgrass; Great Basin; invasion; medusahead; restoration; soil N management.

Introduction

Nonnative invasive annual grasses (hereafter annual grasses) pose serious threats to a number of perennial-dominated ecosystems worldwide (D'Antonio and Vitousek 1992). Ecosystem effects of these invaders include increased fire frequency, altered nutrient cycles, reduced species diversity, as well as reduced quality of forage and wildlife habitat (Hironaka 1961, Facelli et al. 1988, Mack 1989, Whisenant 1990, Evans et al. 2001, Knick et al. 2003, Standish et al. 2007). Given the serious nature of these impacts, it is not surprising that researchers and managers have focused intensively on identifying mechanisms of annual grass invasion as well as strategies for reestablishing native perennial grasses (hereafter perennial grasses) in annual grass-infested areas (e.g., Bureau of Land Management 1999, Chambers et al. 2007).

In nutrient-poor systems dominated by slow-growing perennials, annual grass invasion most commonly has been attributed to increased soil nitrogen (N) availability following disturbance (McLendon and Redente 1991, Kolb et al. 2002, Brooks 2003). Due to their faster growth rates and ability to rapidly take up N, annual grasses are thought to be more competitive than perennial grasses in high-N soils (Melgoza and Nowak 1991, Norton et al. 2007, Vasquez et al. 2008*a*, MacKown et al. 2009) (see Plate 1). In contrast, perennial grasses, with their greater investment in belowground structures and ability to recycle and store N (Chapin 1980, Fargione and Tilman 2002), are thought to be favored under low-N conditions (Vasquez et al. 2008*b*). These trait differences have led to the suggestion that managing soils for low N availability will facilitate reestablishment of native perennial grasses in annual grass-dominated systems

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(Krueger-Mangold et al. 2006, Vasquez et al. 2008*b*, Brunson et al. 2010). Although soil N management is increasingly being presented as a key management strategy for large-scale restoration efforts and invasive plant management programs, (e.g., Prober et al. 2005, Krueger-Mangold et al. 2006, Mazzola et al. 2008) there has been no quantitative synthesis evaluating the degree to which soil N management differentially impacts growth and competitive ability of annual and perennial grasses. Such insight is critical to improving prediction of when soil N management will facilitate perennial grass reestablishment in annual grass-dominated ecosystems.

There is mixed support for soil N management facilitating reestablishment of perennial grasses in annual grass-dominated communities. Carbon addition to annual grass-dominated coastal prairie and old-fields in North America and pasture in Australia lowered soil N availability and facilitated reestablishment of perennial grasses (Alpert and Maron 2000, Paschke et al. 2000, Prober et al. 2005). While these studies did not identify mechanisms associated with species replacement, these results were attributed largely to an overall lower N requirement of perennial grasses or to changes in competitive relationships among species as N availability declined. On the other hand, carbon addition to coastal and interior grasslands, as well as sagebrush steppe communities in North America, lowered soil N availability but did not facilitate reestablishment of perennial grasses (Corbin and D'Antonio 2004, Huddleston and Young 2005, Mazzola et al. 2008). Therefore, while the positive relationship between increased soil N availability and annual grass invasion is well demonstrated, it is not clear that lowering soil N necessarily will allow perennial grasses to reestablish in annual grass-dominated systems.

While some variation in results among studies could be due to site-specific factors, the large variation in the study findings suggests the current framework of managing soil N to restore annual grass-invaded systems may be incomplete. Major advances in understanding trade-offs associated with different plant ecological strategies have been made (Diaz et al. 2004, Wright et al. 2004). Likewise, there has been substantial progress made in understanding processes influencing plant community assembly (e.g., Weiher and Keddy 1999).

Although these lines of research have important implications for understanding the limitations and potential of using soil nutrient management to restore systems dominated by invasive plants, these concepts have not been integrated into applied research and management programs. Integrating these concepts may greatly improve our ability to design restoration strategies for annual grass-dominated systems as well as invasive plant-dominated communities in general.

Research on plant ecological strategies suggests that plant species can be differentiated based on a set of key traits representing a trade-off between resource acquisition and resource conservation (Tilman 1990, reviewed in Aerts 1999, Grime and Mackey 2002). Under this framework, perennial plants are expected to maximize resource conservation by making mechanical and chemical investments in tissue that increase tissue life span and decrease tissue loss due to herbivory or environmental stress (Lambers and Poorter 1992, Westoby et al. 2002, Wright et al. 2004). While these investments decrease relative growth rate (RGR), the conservation strategies increase mean nutrient residence time, allowing a greater duration of return on nutrients captured (Berendse and Aerts 1987). These traits, combined with the ability of perennials to recycle nutrients, make perennials less dependent on soil nutrient pools for growth (Chapin 1980). Over the long term, these traits are expected to give slow-growing perennials an advantage in low-nutrient soils compared to annuals (Berendse 1994, Aerts 1999).

Processes that occur during community assembly, however, may not allow perennial seedlings to survive long enough to realize any benefit from soil nutrient management. The timing of seed arrival, germination, and seedling emergence, as well as seedling growth rate, determines species priority. Priority effects strongly influence plant community assembly (Egler 1952, Ejrnaes et al. 2006, Korner et al. 2008). At the seedling stage, earlier emerging and faster-growing species often are placed at a competitive advantage because it allows these species to preempt resources and allows seedlings to achieve a greater initial size (Verdú and Traveset 2005). The ability of annuals to geminate and emerge earlier than perennials has been well documented (Wilson et al. 1974, Reynolds et al. 2001). In addition, because annuals invest little in tissue protection and defense, over the short term, annuals may achieve greater growth rates than perennials in low-nutrient soils (Ryser and Lambers 1995, Gutschick 1999). Taken together, priority effects and lower tissue construction costs may allow invasive annual grasses to maintain an advantage in low-N soils.

Our broad objective was to use meta-analysis to evaluate the degree to which soil N management differentially impacts growth and competitive ability of annual and perennial grasses. Here we test three hypotheses: (1) Decreasing soil N availability has a greater negative effect on biomass and tiller production of annual compared to perennial grass seedlings. (2) However, seedlings of fast-growing species, including invasive annual grasses, maintain a higher RGR than seedlings of slow-growing species in low-N environments, allowing invasive annual grasses to construct more biomass and tillers than perennials in the short term. (3) As a result, lowering soil N availability will not alter the competitive annual advantage that grass seedlings have over perennial grass seedlings. We then link our results to plant ecological strategy and community assembly theory to improve our ability to

TABLE 1. Studies included in the meta-analysis, grouped by response variable analyzed.

Response variable and no. (fast) (slow) species†	Field (f) or greenhouse (g)	Nitrogen treatment	Soil nitrogen level	
			Low	High
Biomass production				
(3) (3)	g	fertilizer	0.04 mmol/L	4.0 mmol/L
(3) (3)	g	fertilizer	0.02 mmol/L	2.0 mmol/L
(2) (5)	g	straw	0.5 mg/kg	15 mg/kg
(4) (6)	g	straw	2.3 mg/kg	18.6 mg/kg
(1) (3)	g	fertilizer	0 mg/m	10 mg/m
(1) (3)	g	fertilizer	0 mg/kg	280 mg/kg
(1) (3)	g	fertilizer	0.1 mmol/L	1.6 mmol/L
(1) (2)	g	fertilizer	0 mg/kg	220 mg/kg
(1) (2)	g	fertilizer	0.07 mg/kg	0.7 mg/kg
(1) (1)	g	fertilizer	0 mmol/L	8.4 mmol/L
(1) (2)	g	fertilizer	50 mg N	500 mg N
(3) (3)	f	sawdust	0 mg/m^2 sawdust	220 mg/m^2 sawdust
(1) (1)	g	fertilizer	1 mg/L	50 mg/L
Tiller production				
(3) (3)	g	fertilizer	0.04 mmol/L	4.0 mmol/L
(2) (5)	g	straw	2.3 mg/kg	18.6 mg/kg
(3) (3)	g	fertilizer	0.02 mmol/L	2.0 mmol/L
(1) (2)	g	fertilizer	0.07 mg/kg	0.7 mg/kg
Relative growth rate (RGR)				
(2) (2)	g	fertilizer	0.04 mmol/L	4.0 mmol/L
(2) (2)	g	fertilizer	37.5 mmol N/mol	250 mmol N/mol
(2) (2)	g	fertilizer	0.1 mmol/L	24 mmol/L
(1) (1)	g	fertilizer	5 μmol/L	100 μmol/L
(1) (1)	g	fertilizer	0.04 mmol/L	4.0 mmol/L
(2) (2)	g	fertilizer	0.05 mmol/L	5.0 mmol/L
(2) (2)	g	fertilizer	0 ppm	226 ppm
(2) (2)	g	fertilizer	0 mmol/week	3.9 mmol/week
(1) (1)	g	soil type	not reported	not reported
(2) (2)	g	fertilizer	0.05 mmol/L	0.5 mmol/L
Competitive effect				
(1) (1)	g	fertilizer	0 mmol/L	8.4 mmol/L
(1) (1)	g	fertilizer	0 mg/kg	280 mg/kg
(1) (1)	g	fertilizer	0 mg/m^2	10 mg/m^2
(1) (2)	g	fertilizer	50 mg	500 mg
(3) (3)	f	sawdust	0 mg/m^2 sawdust	220 mg/m^2 sawdust
(1) (1)	g	fertilizer	7 μmol/L	326 μmol/L
(1) (1)	g	fertilizer	1 mg/L	50 mg/L
(1) (2)	g	fertilizer	0 mg/m^2	10 mg/m^2

† Number of annual (fast-growing) and perennial (slow-growing) species.
‡ Community types shown as "mixed" were from a range of communities including agronomic, horticultural, and wildland settings.

understand how soil N management may be used to restore annual grass-dominated communities.

METHODS

Analytical approach

We used meta-analysis to test our hypotheses. The first step in meta-analysis involves compiling data from studies that imposed similar treatments. Then results from the studies are statistically synthesized by estimating the size of the treatment effects averaged across studies (Gurevitch and Hedges 1993). In our study, the natural log response ratio (ln RR) was used as the effect size index where $\ln \mathrm{RR} = \ln(T_z/T_b) = \ln T_z - \ln T_b$, and T_z and T_b are means of the response variable for two different treatment groups (Hedges et al. 1999). Therefore, this index estimates the proportional difference between treatment groups. An ln RR of zero indicates the response variables do not vary between groups, and a positive or negative ln RR indicates the response variable is larger for the T_z or T_b group, respectively. The numbers of studies included in the calculation of each effect size parameter are listed in Table 1.

To test our hypotheses regarding N effects on biomass and tiller numbers of annual and perennial grasses, annual grasses served as the T_z group, while perennial grasses served as the T_b group, and effect sizes were calculated for low and high N availability. To test our hypotheses regarding N effects on RGR, the T_z or T_b groups were fast- and slow-growing species, respectively. Here, species classifications are based on their maximum potential RGR under optimal conditions, with fast-growing species achieving a higher RGR under optimal

TABLE 1. Extended.

Community type‡	Reference
sage steppe	James (2008*a*)
sage steppe	J. J. James, *unpublished manuscript*
sage steppe	Monaco et al. (2003*a*)
sage steppe	Monaco et al. (2003*b*)
shortgrass steppe	Lowe et al. (2002)
sage steppe	Vasquez et al. (2008*a*)
eucalypt woodland	Groves et al. (2003)
serpentine grassland	O'Dell and Claassen (2006)
sage steppe	T. A. Monaco, *unpublished manuscript*
sage steppe	Young and Mangold (2008)
oak savannah	Pfeifer-Meister et al. (2008)
coastal prairie	Corbin and D'Antonio (2004)
coastal prairie	Kolb et al. (2002)
sage steppe	James (2008*a*)
sage steppe	Monaco et al. (2003*b*)
sage steppe	J. J. James, *unpublished manuscript*
sage steppe	T. A. Monaco, *unpublished manuscript*
sage steppe	James (2008*b*)
chalk grassland	Van der Werf et al. (1993)
mixed	Fichtner and Schulze (1992)
Mediterranean basin	Garnier et al. (1989)
mixed	Robinson and Rorison (1987)
mixed	Taub (2002)
mixed	Burns (2004)
grass savannah	Reich et al. (2003)
acidic grassland	Higgs and James (1969)
mixed	Shipley and Keddy (1988)
sage steppe	Young and Mangold (2008)
sage steppe	Vasquez et al. (2008*a*)
shortgrass steppe	Lowe et al. (2003)
oak savannah	Pfeifer-Meister et al. (2008)
coastal prairie	Corbin and D'Antonio (2004)
mixed	Claassen and Marler (1998)
coastal prairie	Kolb et al. (2002)
coastal prairie	Abraham et al. (2009)

conditions than slow-growing species. In all cases, classification of each species was assigned by the authors of the primary studies. This data set included fast-growing annual grasses and slow growing perennial grasses but also included data from other functional groups such as forbs. This broad comparison between fast- and slow-growing species was included in our analysis because RGR is a key trait describing ecological variation among species and is a good predictor of invasiveness (Grotkopp et al. 2002, Burns 2004, Grotkopp and Rejmánek 2007). Thus, examining how soil N availability impacts RGR of fast- and slow-growing species in general provides broad insight into the degree to which soil N management may differentially impact growth of native and invasive species.

A similar approach was taken to test our third hypothesis regarding effects of N availability on competitive abilities of annual and perennial grass seedlings. Experimental designs for the competition studies included addition series, simple addition (neighbor present/absent) and replacement series. The calculation of competitive effects differs among designs (Gibson et al. 1999). For example, addition series studies allow for calculation of per plant competitive effects, while simple addition designs allow only for calculation of the competitive effect of having neighbors present. To address this, we calculated effect sizes within each of the three general experimental design types. For the purposes of this study, this was a better option than restricting our analysis to one type of design or losing information by reducing more informative designs to less complex designs (i.e., treating addition series and replacement series designs as simple addition designs). For the addition series studies, the effect size ($\ln \mathrm{RR}$) was calculated as $\ln(\mathrm{RR}) = \ln(\text{biomass of target plant grown with } X + 1 \text{ neighbors}) - \ln(\text{biomass of target plant grown with } X \text{ neighbors})$, where the integer X varies from one to the maximum number of neighbors in the study. For the replacement series studies, the effect size ($\ln \mathrm{RR}$) was calculated as $\ln \mathrm{RR} = \ln(\text{biomass of perennial plant grown with } X \text{ annuals and } Y \text{ perennials}) - \ln(\text{biomass of perennial plant grown with } X + 1 \text{ annuals and } Y - 1 \text{ perennials})$, where the number of plants per pot (i.e., $X + Y$) was held constant. For the simple addition studies the effect size ($\ln \mathrm{RR}$) was calculated as $\ln \mathrm{RR} = \ln(\text{biomass of perennial plants grown with annual neighbors}) - \ln(\text{biomass of perennial plants grown without neighbors})$.

To gain broader insight into what net effect managing soil N has on the growth of perennial target plants grown under competition with annual grass neighbors, we also compared biomass of perennials growing with annuals under high N to biomass of perennials growing with annuals under low N. In this calculation, we used a density of one perennial plant per pot/plot (i.e., pot or plot) and the highest reported annual density from each study. In our effect size index for this comparison, T_z is perennial plant biomass grown with annual grass neighbors under high N, and T_b is perennial plant biomass grown with annual grass neighbors under low N.

Data collection

For our analysis, we used the Web of Science to locate all studies that had the terms "annual, perennial and nitrogen" or "nitrogen and RGR" in the key words, title, or abstract. We also contacted authors of professional society meeting abstracts to access unpublished data. Of the 35 data sets used, only four were unpublished. All studies evaluated plants started from seed. No measurements were made on established plants, so conclusions drawn from the analyses are limited to the seedling stage. We analyzed the raw data when they were available. However, the raw data were not available for all studies, so it was often necessary to analyze the reported means, sample sizes, and standard deviations from the manuscripts. Several of the studies evaluated more than two N levels. For simplicity, we

analyzed the lowest N treatment from each study along with the highest N treatment from each study, provided there were no toxic N responses observed at the highest level.

To test our first hypothesis regarding N effects on biomass and tiller production, a study needed to manipulate N availability and include at least one annual and one perennial grass species. In addition, plant density had to be held constant across N treatments and biomass and tiller production had to be reported on a per plant basis. To test our second hypothesis about N availability and RGR, we used the same criteria developed for the biomass and tiller data but also included studies that compared RGR of fast- and slow-growing species (sensu Lambers and Poorter 1992) under different levels of N availability. To test our third hypothesis about the effect of N availability on competitive interactions of perennial and annual grasses, a study had to experimentally manipulate N availability and annual and perennial grass densities. Taken together, 25 studies met our criteria for at least one of the variables, and some studies provided data for more than one variable, resulting in 35 data sets (Table 1).

Analysis

As is common in meta-analysis, we used regression models to analyze our data (Berkey et al. 1995, Bender et al. 1998) and 95% Bayesian confidence intervals to estimate effect size parameters (van Houwelingen et al. 2002, Gelman et al. 2004). Compared to classical confidence intervals, Bayesian confidence intervals have a simpler interpretation (Berry and Lindgren 1996). Given the modeling assumptions, there is simply a 0.95 probability that our confidence intervals bracket the true ln RR values. We report finite-population confidence intervals, so our estimates reflect average effect sizes for the studies in the data set (Gelman and Hill 2007).

Models for biomass, tillers, and RGR.—We estimated effects of N availability on plant traits with the following hierarchical multiple linear regression model:

$$\ln y_i \sim \mathcal{N}(\alpha_{1,j(i)} + \alpha_{2,j(i)}x_{1,i} + \gamma_{1,j(i)}x_{2,i} + \gamma_{2,j(i)}x_{3,i} + \delta_{l(i)}x_{4,i}, \sigma_{j(i)}) \quad (1)$$

where, depending on the trait being modeled, y_i is either RGR, number of tillers per plant, or biomass per plant in pot i, and $\mathcal{N}(\mu, \sigma)$ is the normal distribution with mean μ, standard deviation σ. The $j(i)$ map data points to studies. For example, if $j(35) = 4$, then the 35th observation is on study 4. The $l(i)$ similarly map data points to levels of the N availability × species × study interaction. The x vectors contain 0s and 1s and control parameter activity. For example, $x_{1,i}$ equals 0 if observation i is on a perennial, because the $\alpha_{2,j(i)}$ are not used in modeling perennials. Depending on the trait being modeled, $\alpha_{1,j(i)}$ is either mean perennial plant biomass under low N, mean perennial tiller density under low N, or mean RGR of slow-growing species under low N. The $\alpha_{1,j} + \alpha_{2,j}$ represent these same means for annuals or fast-growing species. The $\gamma_{1,j}$ and $\gamma_{2,j}$ are study-specific effects of high N availability on perennials (or slow-growing species) and annuals (or fast-growing species), respectively. The δ_l are species × N availability × study interactions, which were included for studies with multiple annual or perennial species, or multiple slow- or fast-growing species. Finally, σ_j is the random error standard deviation for study j. Sample standard deviations were unavailable for five growth rate studies and one biomass study, so we regressed means on standard deviations using the complete data sets and then inferred the missing standard deviations based on the least squares parameter estimates from the regressions.

We used hierarchical Bayesian methods to fit Eq. 1, because these methods have several advantages in meta-analysis (Gelman et al. 2004). In our case, the advantages included mechanisms for incorporating all important sources of uncertainty, ease of model fitting when only the treatment means, sample sizes, and dispersion statistics were available (i.e., when the raw data were unavailable), and the availability of Markov chain Monte Carlo algorithms for calculating all desired functions of the model parameters. The Bayesian approach requires assigning prior distributions to the model parameters, and we used standard, noninformative priors (Gelman et al. 2004). The five regression parameter groups (i.e., $\alpha_{1,j}$, $\alpha_{2,j}$, $\gamma_{1,j}$, $\gamma_{2,j}$, and δ_l) were assigned normal distributions with each group having its own mean μ and standard deviation τ. All μ and τ were assigned uniform distributions, except for the mean of the δ vector, which was set to 0. Priors on random error variances were $p(\sigma_j^2) \propto 1/\sigma_j^2$. All marginal posterior distributions were in closed form, so we constructed a Gibbs sampler in FORTRAN and used it to simulate the joint posterior distributions (Intel Corporation 2003). We assessed convergence using the methods of Gelman and Rubin (1992).

Competition models.—Because the competition studies used differenxperimental designs, different models were used depending on the experimental design. We fit the following multiple linear regression model to the addition series data sets of Young and Mangold (2008):

$$\ln y_i \sim \mathcal{N}\left(\sum_{k=1}^{K-2} \beta_k x_{k,i} + \beta_{K-1}x_{K-4,i}x_{K-3,i} + \beta_K x_{K-4,i}x_{K-2,i}, \sigma\right) \quad (2)$$

where, depending on the plant group being modeled, y_i is either mean biomass per annual plant or mean biomass per perennial plant in pot i. The first parameter in the summation is the intercept, and other summation terms control for replication main effects in both studies as well as the main effects of phosphorus and experiment in the two-experiment study of Young and Mangold

(2008). Elements of x_{K-4} equal 1 for high-N pots and 0 for low-N pots, and x_{K-3} and x_{K-2} contain the perennial and annual plant densities, respectively. This being the case, $\beta_{k-2}x_{K-2}$, $\beta_{k-3}x_{K-3}$, and $\beta_{k-4}x_{K-4}$, correspond to main effects of competition and N availability. Finally, β_{K-1} describes the N × perennial plant density interaction, and β_K describes the N × annual plant density interaction.

Eq. 2 is statistically identifiable only for studies that vary annual plant densities independently of perennial plant densities. For the six competition studies that did not independently vary densities, we used the following multiple linear regression model:

$$\ln y_i \sim \mathcal{N}\left(\sum_{k=1}^{K-1} \beta_k x_{k,i} + \beta_K x_{K-2,i} x_{K-1,i}, \sigma\right) \quad (3)$$

where y_i is mean biomass per perennial plant in pot/plot i, and the first parameter in the summation is the intercept. With Pfeifer-Meister et al. (2008) and Corbin and D'Antonio (2004), some summation terms model species effects, because these studies contained multiple annual and/or perennial species. The $x_{K-2,i}$ equal 1 for high-N pots/plots and 0 for low-N pots/plots. In the four replacement series studies, $x_{K-1,i}$ is the number of annuals in pot i (Claassen and Marler 1998, Kolb et al. 2002, Lowe et al. 2003, Pfeifer-Meister et al. 2008), and in the two other studies, $x_{K-1,i}$ equals 0 or 1 if annuals were absent or present, respectively (Corbin and D'Antonio 2004, Abraham et al. 2009). The β_K parameter models the N × annual abundance interaction. The sample standard deviation was unavailable for Claassen and Marler (1998), so we used the approach described above to infer the standard deviation. We used Bayesian statistics to fit Eqs. 2 and 3 because Gibbs sampling was useful for averaging the confidence intervals over the different studies and simulating nonstandard functions of the model parameters. However, although we used Bayesian methods to fit the models, our parameter estimates coincide with the classical regression results because of our choice of prior distributions (Gelman et al. 2004).

Results

The data support our first hypothesis that decreasing soil N availability has a greater negative effect on biomass and tiller production of annual compared to perennial grass seedlings. Confidence intervals on biomass differences (annual − perennial) for high and low N do not overlap (Fig. 1A). Therefore, reducing soil N decreased annual grass biomass by a greater proportion than perennial grass biomass. Confidence intervals support the same conclusion for tillers, but confidence intervals overlap appreciably so that the evidence is weaker (Fig. 1B).

The data also support our second hypothesis regarding RGR of fast- and slow-growing species and tillers and biomass production of annual and perennial grasses in low-N environments. The confidence interval on the RGR difference (fast-growing species − slow-growing species) is >0 for low N (Fig. 1C). Therefore, species with high inherent growth rates under optimal conditions also maintained higher growth than inherently slow-growing species when N availability was low. Moreover, confidence intervals on tiller and biomass differences (annual − perennial) are also greater than 0 for low N (Fig. 1A, B), so annual grasses produced more

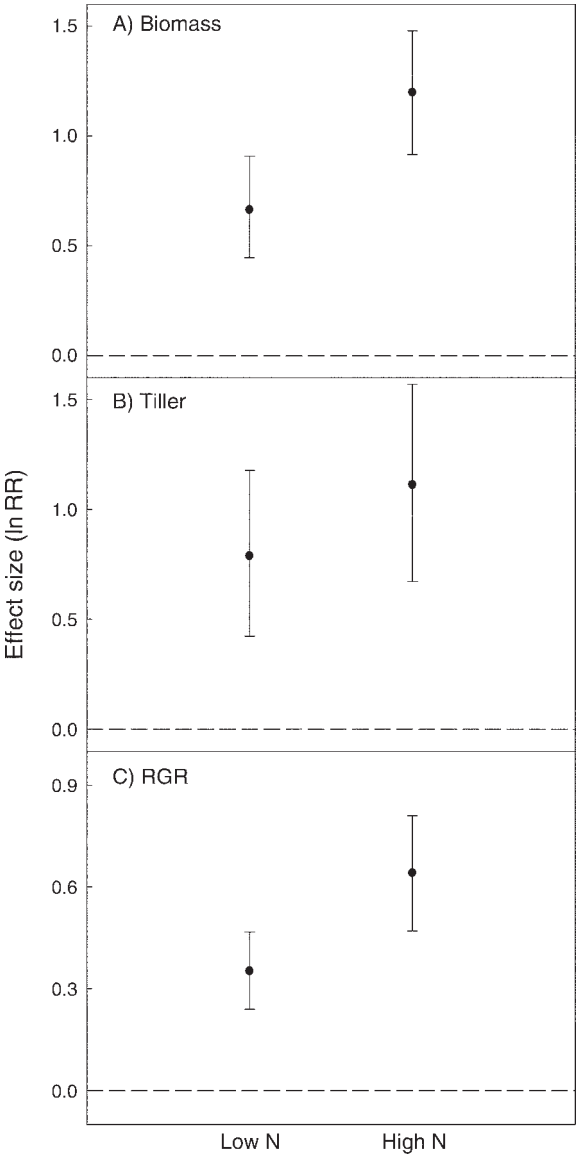

FIG. 1. Most likely parameter values (solid circles) and 95% confidence intervals (vertical bars) on log response ratios (ln RR) where (A) ln RR = ln(perennial mass per plant) − ln(annual mass per plant), (B) ln RR = ln(perennial tillers per plant) − ln(annual tillers per plant), and (C) ln RR = ln(RGR of fast-growing species) − ln(RGR of slow-growing species). RGR is relative growth rate. Intervals estimate means over 14, 4, and 8 studies for biomass, tillers, and RGR, respectively.

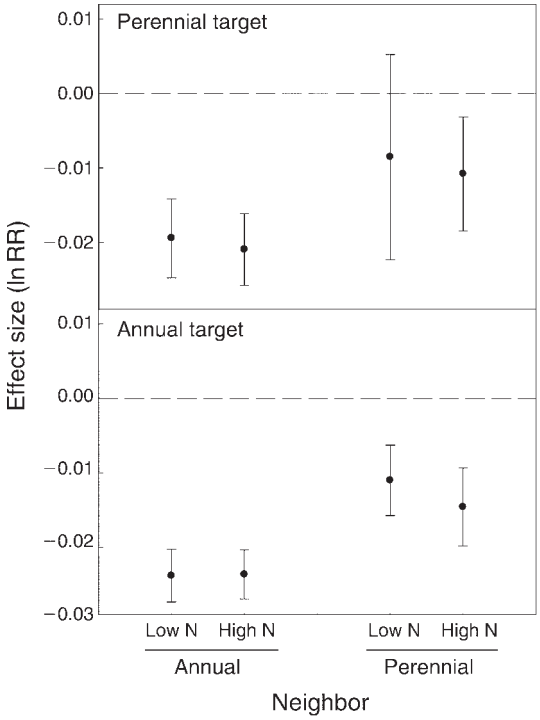

FIG. 2. Most likely parameter values (solid circles) and 95% confidence intervals (vertical bars) on log response ratios (ln RR). The effect sizes (ln RR) describe changes in target plant biomass resulting from increasing neighbor density by one plant per pot. Specifically, ln RR = ln(biomass of target plant grown with $X+1$ neighbors) − ln(biomass of target plant grown with X neighbors), where the integer X varies from 1 to the maximum number of neighbors in the study. Data are from addition series studies that manipulated annual and perennial grass densities and N availability (Vasquez et al. 2008*a*, Young and Mangold 2008).

biomass and tillers than perennial grasses when N availability was low.

The data support our third hypothesis that lowering soil N availability will not alter the competitive advantage annual grass seedlings have over perennial grass seedlings. While all point estimates of competition parameters are negative, indicating that plants competed under low and high N, confidence intervals for low and high N in the addition series studies (Fig. 2), the replacement series studies (Fig. 3A), and the simple addition studies (Fig. 3B) overlapped substantially, suggesting N availability had little effect on competition intensity. Moreover, the addition series studies showed that annual grass neighbors had a stronger competitive effect on both annual and perennial targets compared to perennial neighbors, and that the competitive effects of annual neighbors on perennials did not decrease with lower N availability (Fig. 2).

Perennial targets competing with annual grass neighbors did not incur a net cost in biomass production in high-N environments (Fig. 4). Point estimates and confidence intervals describing the difference in perennial plant biomass when perennial plants were grown with annual neighbors under high N compared to when perennial plants were grown with annual grass neighbors under low N were positive for the addition series and replacement series studies. This indicates that perennials produced more biomass when grown with annual grass competitors under high N compared to when grown with annual grass competitors under low N. Confidence intervals from the simple addition studies were centered on zero, so data from these studies were inconclusive about the effect of soil N on perennial biomass production.

DISCUSSION

The current soil N management framework rests on the assumption that because increasing N availability facilitates invasion, decreasing N availability should

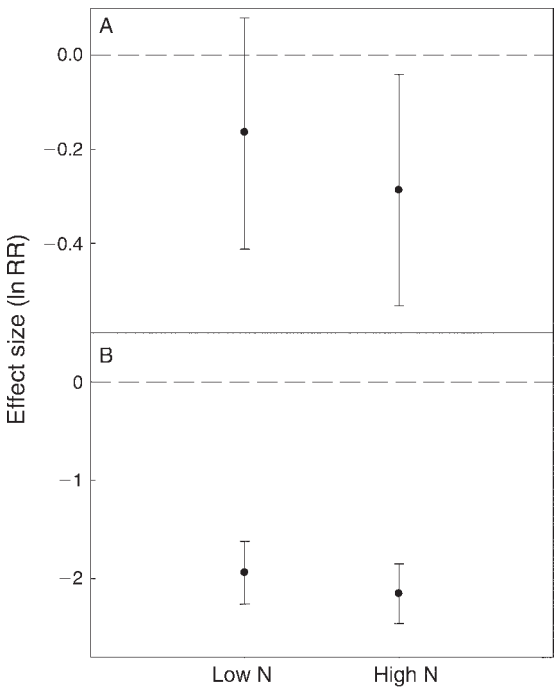

FIG. 3. Most likely parameter values (solid circles) and 95% confidence intervals (vertical bars) on log response ratios (ln RR). (A) The ln RR describes the change in perennial grass biomass resulting from replacing one perennial neighbor with one annual neighbor in greenhouse pots. Specifically, ln RR = ln(biomass of perennial plant grown with X annuals and Y perennials) − ln(biomass of perennial plant grown with $X+1$ annuals and $Y-1$ perennials), where the number of plants per pot (i.e., $X+Y$) was held constant. Data are from replacement series studies that manipulated annual and perennial grass densities as well as N availability (Claassen and Marler 1998, Kolb et al. 2002, Lowe et al. 2003, Pfeifer-Meister et al. 2008). (B) The ln RR describes effects of annual grasses on perennial grass biomass. Specifically, ln RR = ln(biomass of perennial plants grown with annual neighbors) − ln(biomass of perennial plants grown without neighbors). Data are from simple addition studies that manipulated N availability and grew perennial grasses with and without annual neighbors (Corbin and D'Antonio 2004, Abraham et al. 2009).

facilitate restoration of systems dominated by invasive annual plants (McLendon and Redente 1992, Alpert and Maron 2000, Blumenthal et al. 2003). At the seedling stage we found no evidence to support this assumption. In support of our first hypothesis, annual grasses demonstrated a greater decrease in biomass and tiller production than perennial grasses as soil N availability declined (Fig. 1A, B). However, in support of our second hypothesis, annual grasses maintained higher RGR and produced more biomass and tillers than perennial grasses under low N availability (Fig. 1). Consistent with these results and our third hypothesis, we found no evidence that lowering N availability fundamentally alters competitive interactions between annual and perennial grasses. Across competition studies, lowering N did not reduce competitive effects of annual neighbors on perennial targets (Figs. 2 and 3). Moreover, our analysis provides no evidence that perennial plants growing with annual competitors benefited from reductions in N availability. In the addition and replacement series designs, perennial plants growing with annual grass competitors clearly produced more biomass in high- than low-N environments (Fig. 4). If perennial seeds can germinate and reach the seedling stage when competing with annual grasses, these observations suggest that high N availability may provide perennials a fitness advantage even with annual grasses present.

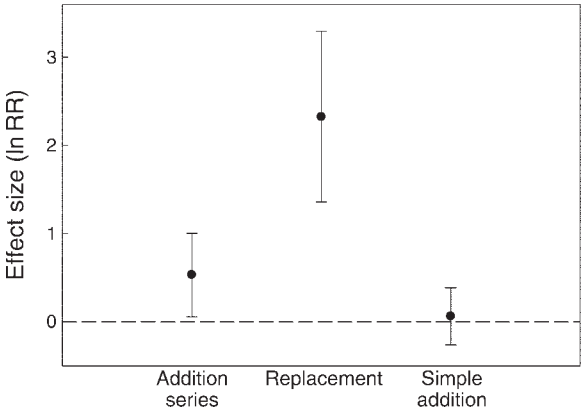

FIG. 4. Most likely parameter values (solid circles) and 95% confidence intervals (vertical bars) on log response ratios (ln RR). The ln RR describes effects of N availability on biomass production of perennial grasses growing with annual grasses. Specifically, ln RR = ln(biomass of perennial plants grown with annual grasses under high N) − ln(biomass of perennial plants grown with annual grasses under low N). The estimates were derived using the highest annual grass density reported by each study. Separate estimates are provided for addition-series study designs (Vasquez et al. 2008*a*, Young and Mangold 2008), replacement-series study designs (Claassen and Marler 1998, Kolb et al. 2002, Lowe et al. 2003, Pfeifer-Meister et al. 2008), and simple-addition study designs (Corbin and D'Antonio 2004, Abraham et al. 2009).

Extrapolating results from growth and competition studies conducted under controlled experimental conditions to the field needs to be done with caution for several reasons. First, soil N availability influences multiple processes, including those associated with bacteria and fungal communities and seed germination (Karssen and Hilhorst 1992, Klein et al. 1996). These processes are not necessarily captured in short-term greenhouse studies, but may play a large role in ultimately determining effects of soil N management on restoration. Second, previous meta-analyses on plant interactions have shown that results can vary depending on the choice of response variable (Goldberg et al. 1999). The studies available for this analysis all reported biomass, and it is possible that soil N management might have a different effect on survival. Third, previous work also has shown that outcome and intensity of plant interactions do not necessarily equate to the importance of these interactions for structuring populations and communities (Lamb and Cahill 2008). Fourth, other biotic and abiotic factors also influence the outcome of plant interactions. For example, herbivory was not manipulated in any of these studies, and herbivores can mediate plant interactions (Fraser and Grime 1999). Likewise, water availability, temperature, and micronutrients can influence interactions between invasive annual grasses and native plants (Bradford and Lauenroth 2006, Chambers et al. 2007, Adair et al. 2008). Lastly, it is important to note that the bulk of the studies used in this analysis tended to focus on dominant native and invasive species, so the number of species represented in the analysis is limited, and it is possible that soil N management could provide a benefit for some species in some systems.

Nevertheless, our results provide insight into the role soil N management will have on growth and interaction of annual and perennial grass seedlings. In restoration scenarios in which annual and perennial grasses are interacting as seedlings, our analyses indicate that soil N management alone will not directly facilitate establishment of native perennial grasses in terms of growth and initial competitive ability. While this conclusion is supported by a number of studies showing that soil N management failed to facilitate restoration of systems dominated by invasive plants (e.g., Corbin and D'Antonio 2004, Huddleston and Young 2005, Mazzola et al. 2008), other studies have demonstrated that soil N management facilitates restoration of systems infested by a range of invasive plants (e.g., Alpert and Maron 2000, Paschke et al. 2000, Prober et al. 2005). A critical question to answer then is can we use results from this analysis to provide insight into these discrepancies and improve our ability to understand the conditions allowing soil N management to facilitate restoration of annual grass-infested systems?

Linking the soil N management framework to plant strategy and community assembly theory

Plant ecological strategy and community assembly theory provide the foundation for advancing our ability

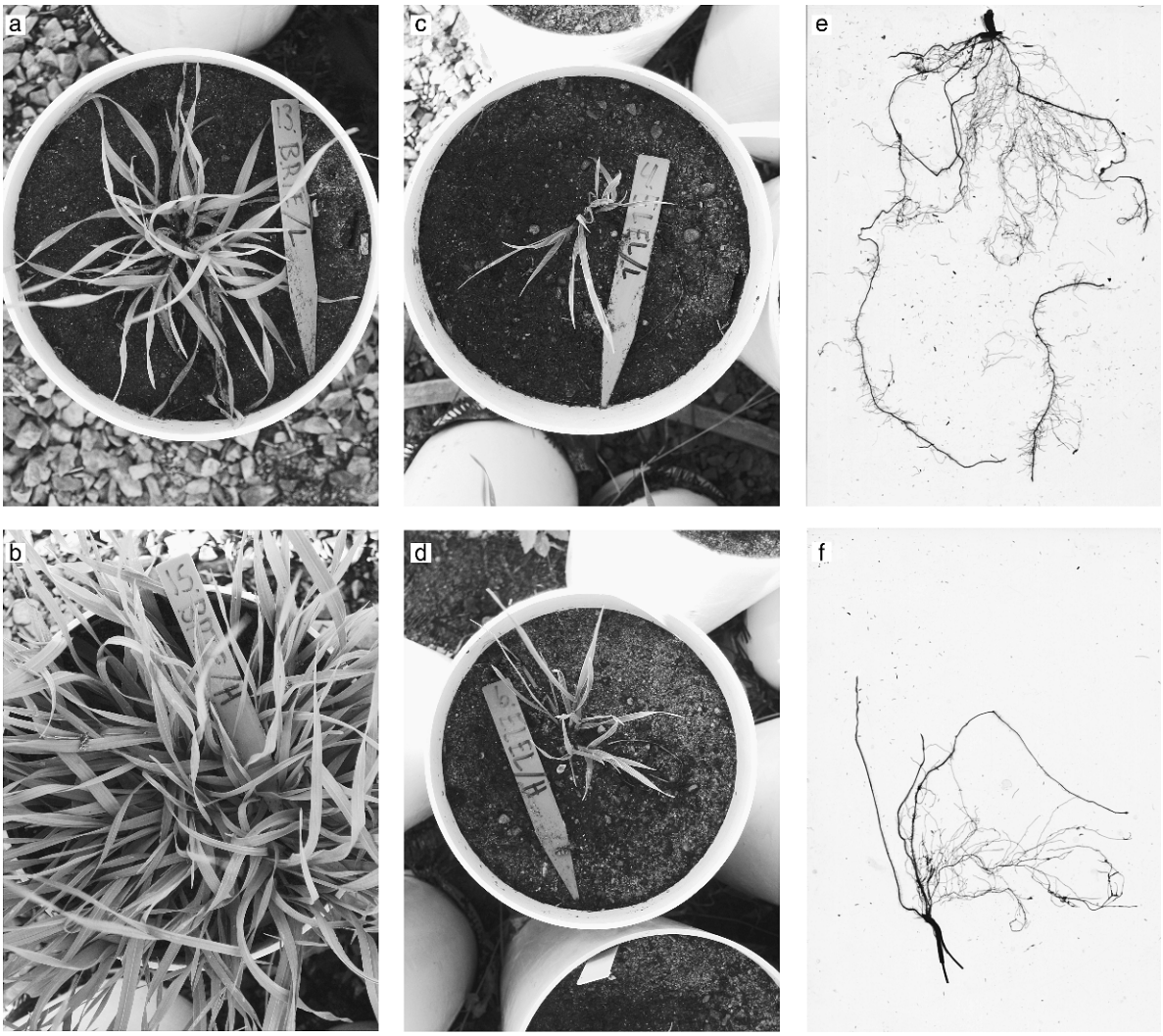

PLATE 1. Aboveground biomass production of the invasive annual grass *Bromus tectorum* in (a) low-N and (b) high-N soil; aboveground biomass production of the native perennial *Elymus elymoides* in (c) low-N and (d) high-N soil; and root length production of (e) *B. tectorum* and (f) *E. elymoides* in low-N soil. Photo credits: J. J. James.

to understand and predict how soil N management may influence restoration outcomes. For example, RGR has long been a key trait used to characterize different plant ecological strategies (e.g., Grime 1977, Goldberg and Landa 1991, Loehle 2000). Specific leaf area (SLA) is the principal trait influencing RGR variation among species (Lambers and Poorter 1992). Morphological and chemical adjustments that protect leaf tissue from abiotic stress or herbivores decrease SLA and consequently, RGR (Poorter et al. 2009). While reducing SLA indirectly reduces growth and resource capture, it increases resource conservation by increasing leaf life span. A high SLA, on the other hand, results in rapid resource capture but poor resource conservation due to shorter leaf life span (Westoby et al. 2002).

While resource conservation strategies are expected to become increasingly important as soil N availability declines, favoring low-SLA species, our meta-analysis demonstrated that fast-growing, high-SLA species, including invasive annual grasses, maintained greater growth rates in low-N soils than slow-growing species. These differences in initial RGR resulted in greater biomass and tiller production by annual grass seedlings in low-N soils compared to perennials. Annuals construct thinner and less dense leaves than perennials (Garnier 1992, Ryser and Lambers 1995). As a result, annuals produce more leaf area per unit biomass allocated to leaves, allowing annuals to grow faster than perennials. At the seedling stage, this difference in tissue construction cost allows annuals to preempt more belowground resources than perennials in nutrient-poor soils (James 2008*a*). Our meta-analysis combined with these tissue construction cost considerations suggests slow-growing perennials have no direct advantage in

terms of initial growth in low-N soils compared to invasive annual grasses. Consequently, if processes occurring during the seedling establishment phase largely drive plant community composition, then soil N management likely will not influence restoration outcomes.

Plant community composition and restoration outcomes, however, also are influenced by longer-term processes, not just processes associated with seedling establishment. Internal plant nutrient recycling, for example, contributes significantly to the long-term performance of perennials in low-N soils (Killingbeck and Whitford 1996). While annual plants must depend entirely on soil nutrient supplies to support biomass production, perennials can rely on nutrients that were translocated and stored following tissue senescence. Perennials also can conserve nutrients by investing heavily in structural support for leaf and root tissue (Garnier 1992, Roumet et al. 2006). Nutrient recycling and investment in long-lived tissue ultimately lowers the amount of soil nutrients a perennial plant needs to acquire (Berendse and Aerts 1987). However, these traits come at cost. Perennials must invest carbon resources into storage and tissue protection, causing an unavoidable decrease in growth (Bloom et al. 1985). In contrast, annual plants, which do not have the same carbon costs, can reinvest proportionately more fixed carbon into more leaf area and thus more quickly realize returns on their carbon investment. While traits associated with nutrient recycling may be advantageous to perennials in the long term, at the seedling stage these traits may actual place perennials at a disadvantage in nutrient-poor soils. Because of these differences in nutrient conservation traits between annuals and perennials, the benefits of soil N management will be a function of time, with N management providing little benefit initially but providing greater benefit as time progresses. As a consequence, the benefits of soil N management will depend on how the initial competitive environment is managed.

Differences in priority among species strongly influence the initial competitive environment and the successional trajectories of plant communities (Chase 2003, Korner et al. 2008). Early germination and rapid growth of annuals compared to perennials long have been recognized as central barriers to restoration of annual grass-infested systems (Major and Pyott 1966, Harris 1967, Humphrey and Schupp 2004). Priority effects allow annuals to grow larger during seedling establishment, providing a competitive advantage during early phases of community assembly (Fowler 1984, Connolly and Wayne 1996). Because competition for soil resources is size symmetric (Weiner and Damgaard 2006), even in low-N soils the priority effect and greater growth rate expressed by annuals allows them to preempt more resources. If competitive outcomes are determined mainly by resource capture differences, then soil N management will have little effect on revegetation efforts unless priority effects are first successfully controlled.

Management implications: improving the soil N management framework

Theoretical and empirical work has established a positive relationship between resource availability and habitat invasibility (Huenneke et al. 1990, Stohlgren et al. 1999, Davis et al. 2000). For annual grasses, these observations have led to the hypothesis that managing soils for low N availability should facilitate restoration of systems dominated by invasive plants (Alpert and Maron 2000, Krueger-Mangold et al. 2006, Vasquez et al. 2008*b*). A number of studies have explicitly tested this hypothesis with varying results. By considering our results, however, within the context of plant ecological strategies and community assembly processes, we can formulate insight and predictions about how and when soil N management will benefit restoration. Although our analysis focused on invasive annual grasses, these conclusions and predictions should apply to a range of invasion scenarios, particularly when natives and invaders are well differentiated along the ecological spectrum of rapid resource capture vs. effective resource conservation.

In the restoration scenario where native perennials and invasive annuals recruit from seed, lowering soil N is unlikely to positively influence growth and initial competitive ability of native perennials compared to invasive annuals. In this situation, perennials essentially function as annuals during the first growing season and cannot capitalize on key traits that provide them an advantage in low-N soils, such as the ability to remobilize and recycle stored nutrients. Instead, in low-N soils where both annuals and perennials are establishing from seed, priority effects and the ability to maintain a higher RGR give annuals an advantage over perennials. However, restoration outcomes are not driven solely by these short-term individual plant processes. Research that links these patterns of individual plant responses to longer-term population and community-level processes are needed for a complete understanding of how soil N management influences restoration outcomes. In addition, if propagule pools and priority effects of annual grasses can be successfully managed the first year, then soil N management is likely to facilitate restoration. Under these conditions, traits that allow perennials to conserve and recycle nutrients can begin to operate and allow perennials to build nutrient reserves. Over time, these traits should give perennials a competitive advantage over annuals in N-poor soils. While there are a number of potential tools that can manipulate priority effects of annual grasses, including preemergent herbicide, bio-control, mowing, and grazing, there is almost no information about how these tools actually influence ecological processes such as priority effects, interference, and native perennial plant survival. Evaluating how these tools influence

these processes at appropriate spatial and temporal scales and integrating these tools into soil N management programs is the next critical step needed to understand how we can use these conceptual advances in invasion ecology to make practical improvements to restoration programs.

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