Can resource-use traits predict native vs. exotic plant success in carbon amended soils?

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Abstract. Productivity in desert ecosystems is primarily limited by water followed by nitrogen availability. In the deserts of southern California, nitrogen additions have increased invasive annual plant abundance. Similar findings from other ecosystems have led to a general acceptance that invasive plants, especially annual grasses, are nitrophilous. Consequently, reductions of soil nitrogen via carbon amendments have been conducted by many researchers in a variety of ecosystems in order to disproportionately lower invasive species abundance, but with mixed success. Recent studies suggest that resource-use traits may predict the efficacy of such resource manipulations; however, this theory remains largely untested. We report findings from a carbon amendment experiment that utilized two levels of sucrose additions that were aimed at achieving soil carbon to nitrogen ratios of 50:1 and 100:1 in labile sources. Carbon amendments were applied once each year, for three years, corresponding with the first large precipitation event of each wet season. Plant functional traits measured on the three invasive and 11 native herbaceous species that were most common at the study site showed that exotic and native species did not differ in traits associated with nitrogen use. In fact, plant abundance measures such as density, cover, and biomass showed that carbon amendments were capable of decreasing both native and invasive species. We found that early-germinating species were the most impacted by decreased soil nitrogen resulting from amendments. Because invasive annuals typically germinate earlier and exhibit a rapid phenology compared to most natives, these species are expected to be more competitive than native annuals yet more susceptible to early-season carbon amendments. However, desert annual communities can exhibit high interannual variability in species composition and abundance. Therefore, the relative abundance of native and invasive species at the time of application is critical to the success of carbon amendments at our study site. For land management purposes, carbon amendments remain relatively impractical and may only be useful at small scales or in conjunction with other invasive species removal techniques.

Key words: Bromus madritensis; California (USA); competition; Erodium cicutarium; *functional traits; invasive plants; Mojave Desert; nitrophilous; phenology; postfire; restoration;* Schismus barbatus.

INTRODUCTION

Invasive species often thrive in resource-rich environments (Sher and Hyatt 1999, Davis et al. 2000, Daehler 2003, Theoharides and Dukes 2007). Anthropogenic changes to the global nitrogen (N) cycle through agriculture and the combustion of fossil fuels (Vitousek et al. 1997, Townsend et al. 2010) therefore have enormous consequences for the establishment and persistence of invasive species. Nitrogen additions have been found to stimulate the growth of exotic species in a number of systems, including grasslands (Huenneke et al. 1990, Blicker et al. 2002, Gross et al. 2005), tropical forests (Ostertag and Verville 2002, Funk 2008), coastal sage scrub (Padgett and Allen 1999), and desert ecosystems (Brooks 2003, Allen et al. 2009). Thus, a decrease in nitrogen availability should reduce exotic species dominance and may enhance the growth of native vegetation (Perry et al. 2010).

One promising treatment for native annual restoration is the use of a soil carbon amendment. Adding carbon (i.e., sugar or sawdust) to the soil stimulates microbial growth, which immobilizes nitrogen in the new microbial biomass (Jonasson et al. 1996, Zink and Allen 1998, Corbin and D'Antonio 2004). As a result, less nitrogen in the form of NO_3 and NH_4 is available for plant uptake (Wilson and Gerry 1995, Alpert and Maron 2000). The duration and degree to which carbon amendments alter inorganic N pools varies dramatically depending on the type of carbon utilized, and based on ecosystem characteristics such as species composition, climate, soil properties, and other variables (reviewed in Alpert 2010, Perry et al. 2010). Several studies have

found that N availability can return to pre-amendment levels within one year after carbon amendments cease (Alpert 2010). Ideally, a carbon amendment would be most effective if it promoted low-N species that generate plant soil feedbacks that further increase immobilization (Perry et al. 2010).

Carbon additions have been used to reduce exotic species dominance in grasslands and old fields (Reever Morghan and Seastedt 1999, Blumenthal et al. 2003, Corbin and D'Antonio 2004, Suding et al. 2004, Bleier and Jackson 2007, Sanders et al. 2007) and coastal shrublands (Zink and Allen 1998, Alpert and Maron 2000, Cione et al. 2002). Fewer studies have examined the efficacy of carbon additions in desert systems. In the Chihuahuan and Mojave deserts, carbon additions have been effective at increasing soil microbial immobilization of inorganic nitrogen from interspace and understory soils (Gallardo and Schlesinger 1995, Schaeffer et al. 2003). To our knowledge, no studies have applied carbon additions to control invasive annuals in these deserts. Because nitrogen is limiting to desert annual plants only behind water (Gutierrez and Whitford 1987), carbon amendments show promise as a useful treatment for this purpose (Grantz et al. 1998).

In order for soil N manipulation to simultaneously exclude invasive species and promote native species, native and invasive species must differ in traits governing the use of N (Funk et al. 2008). Specifically, invasive species must have a higher N requirement and lower carbon assimilation per unit of N (nitrogen use efficiency, NUE). Many studies support the idea that invasive species are more nitrophilous than natives (Huenneke et al. 1990, Burke and Grime 1996, Davis et al. 2000, Daehler 2003, Suding et al. 2004, Gross et al. 2005), and there has been much work showing that natives adapted to resource-poor environments display resource conservation traits, such as slow growth, low tissue nutrient content, and low rates of carbon assimilation and transpiration (Chapin 1980, Vitousek 1982, Coley et al. 1985). These findings lead to the prediction that native species that require lower amounts of nitrogen should be less affected by carbon addition treatments than nitrophilous invasive species. However, few studies have utilized trait data from invasive and native species for the purpose of directing ecological restoration in invaded systems (Brudvig and Mabry 2008, Wolters et al. 2008, Funk and McDaniel 2009), particularly with respect to resource-use traits.

In this study, we lowered soil N availability via carbon amendments to assess the efficacy of this technique as a restoration tool in a desert ecosystem dominated by annual species. We also evaluated a number of plant traits pertaining to N acquisition and use by three dominant invasive species and 11 native species. Because previous work has shown that N additions in this system stimulate the growth of exotic species (Brooks 2003), we hypothesized that (1) native and invasive species have different N-use traits with invasive species being more nitrophilous than native species, and (2) N immobilization has an asymmetric impact on the cover of invasive and native plant species, affecting nitrophilous invasive grasses disproportionately more than native annuals. Because species with lower N requirements or more efficient use of N should have higher percent cover in carbon addition treatments, N-use traits may provide a predictive means of evaluating the utility of resource manipulation as a restoration strategy.

We conducted our study in a southern California desert shrubland that has elevated soil nitrogen due to recent fire (Raison 1979) and exposure to anthropogenic nitrogen deposition (Fenn et al. 2003, Tonnesen et al. 2007, Rao et al. 2009). Increasing soil nitrogen has been shown to promote exotic annual grasses over native desert forbs (Brooks 2003, Rao and Allen 2010). Therefore, decreasing soil nitrogen with carbon amendments should significantly reduce short-lived nitrophilous (nitrogen-loving) plants, such as exotic annual grasses, and consequently promote native desert species, which are thought to be adapted to low soil nitrogen (Brooks 2003).

METHODS

The study site was located in burned creosote bush scrub at Big Morongo Canyon Preserve (BMCP) in Morongo Valley, San Bernardino County, California, USA. The area receives 5–10.5 kg·ha^{-1}·yr^{-1} of anthropogenic N deposition according to modeled values (Tonnesen et al. 2007, Rao et al. 2009). This site burned in June 2005 in a fire that was primarily fueled by the invasive annual grass, *Bromus madritensis* ssp. *rubens* (red brome). BMCP is located on the western edge of the Little San Bernardino Mountains and is in a transitional zone between the Mojave Desert to the north and the Sonoran (Colorado) Desert to the south. The elevation is ~780 m. Soils are loamy and contain no carbonates (R. J. Steers, *unpublished data*). Average precipitation in the adjacent town of Morongo Valley is 19.6 cm with average snowfall of 8.4 cm. About 85% of average precipitation occurs from October through April (WRCC 2010). Precipitation in the 2004–2005 wet season, which preceded this study, was one of the highest on record. No data were available from the study site in Morongo Valley but from Palm Springs, ~12 km to the south, winter precipitation (October through April) was 281% of normal (WRCC 2010). Precipitation during the experiment was 15.6, 1.2, and 18.9 cm from October through April during the first three seasons (2005–2006, 2006–2007, and 2007–2008) following the fire in June 2005, based on a weather station at BMCP. No snowfall was recorded during this period and summer precipitation was scant (Fig. 1).

In the first postfire wet season (2005–2006), precipitation was slightly below average and irregularly distributed, with occasional long rain-free periods in December and January (Fig. 1). In the second season (2006–2007), little rain fell so that no annual plants
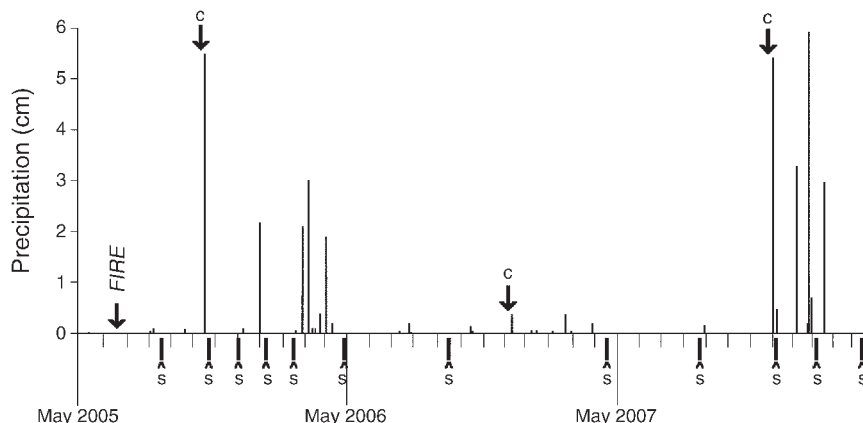
FIG. 1. Precipitation during the experiment in the Big Morongo Canyon Preserve, California, USA. The *x*-axis starts on 1 May 2005 and stops on 30 April 2008. The date of the June fire is indicated (*FIRE*), as are the dates when carbon addition treatments (c) were applied coinciding with the first storm of each wet season, and the dates when soils were sampled (s) for microbial biomass and/or nutrients.

germinated. In the third season (2007–2008), the amount of precipitation was average but it occurred almost entirely within December and January (Fig. 1). Exotic annual grasses were especially abundant in the first year of this study, possibly benefiting from the high rainfall of the preceding season. However, by the third year, exotic annual grasses were less abundant. Native annuals on the other hand, were less common in the first season but more abundant in the third season. For additional information about the study site and its climate see Steers and Allen (2009).

Experimental design

Twelve blocks were placed within the burned creosote bush scrub community using a stratified random sampling scheme. Each block contained three sampling units where a control and two carbon addition treatments were assigned using a randomized block design. Sample units were placed in areas with flat terrain (0–5°) that were mostly interspace (devoid of shrubs) before the fire to avoid heterogeneity due to fertile islands (Adams et al. 1970, Titus et al. 2002). Each sampling unit contained two plots; one was 1.5×1.5 m^2 and the other was 1.5×0.75 m^2 (Fig. 2). Within each plot, a single 1×0.5 m^2 quadrat (sampling frame) was placed inside, allowing for at least a 10-cm buffer with each plot edge. This quadrat was used to nondestructively sample vegetation cover by species and was permanently demarcated using wooden stakes placed on the outside of the quadrat. Within each 1×0.5 m^2 quadrat, an unmarked, relatively small quadrat (0.5×0.25 m^2) would be placed in the middle to nondestructively sample plant density by species each year. All other areas within the larger plot, but outside of the 1×0.5 m quadrat and its buffer, were treated identically (same amount of carbon amendment) but sampled/harvested destructively for plant biomass and soil throughout the experiment (Fig. 2). Any time plant

biomass or soils were collected, the area destroyed was marked so that future sampling would avoid the disturbed area (Fig. 2).

Sucrose was chosen as the carbon amendment because it is labile and rapidly available to soil microbes (Shaban et al. 1998, Magill and Aber 2000). Furthermore, desert systems are characterized as being highly pulsed, where biological processes are tightly coupled to precipitation events (Noy-Meir 1973, Vishnevetsky and Steinberger 1997, James et al. 2006). Thus, the labile nature of sucrose is ideal for use in this system. Another reason why we chose sucrose was because it does not add persistent organic matter to desert soils. Organic matter and decomposition rates are both low in arid ecosystems (Nash and Whitford 1995, Murphy et al. 1998) so using a more recalcitrant carbon amendment, like sawdust or mulch, could alter soil properties in an undesirable way.

Two sucrose levels were used to achieve a soil carbon to nitrogen ratio of 50:1 (carbon) and 100:1 (high carbon) based on labile sources of C and N (NO_3^- and
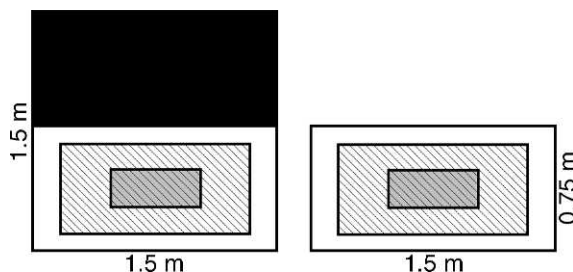

FIG. 2. Schematic of a sampling unit. Each sampling unit contained two plots where the same treatment was applied to the entire area. In the large plot (1.5×1.5 m^2), half of the space (black) was used to harvest soil and plant biomass. The other half of the large plot in addition to the smaller plot (0.75×1.5 m^2) were used to nondestructively sample plant cover in 0.5×1 m^2 quadrats (diagonal-hatch rectangle) and plant density in 0.25×0.5 m^2 quadrats (gray rectangle). White spaces around the larger quadrat represent buffer areas.

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TABLE 1. Bulk density, inorganic nitrogen, and the calculated carbon amounts that were applied to plots in the Big Morongo Canyon Preserve, California, USA.

Year applied	Bulk density (g/cm^3)	Inorganic nitrogen (ppm)	Carbon applied $(g\ C/2.25\ m^2)$
Carbon high (100:1 labile C:N)			
2005	1.27	16.1	547.6
2006	1.51	9.4	381
2007	1.36	6.7	242.6
Carbon low (50:1 labile C:N)			
2005	1.27	16.1	273.8
2006	1.63	9.2	200.8
2007	1.43	8.2	157.4

Note: Data are summer dry season bulk density and inorganic nitrogen (NO_3^- plus NH_4^+) and the corresponding amount of sucrose applied at the beginning of each wet season (see Fig. 1 for dates) to achieve "labile" C:N ratios of 100:1 (carbon high) and 50:1 (carbon low) for large plots (150 cm height $\times$ 150 cm width $\times$ 5 cm depth).

NH_4^+). Hence, this is a "labile C:N" approach and was not meant to actually achieve C:N ratios of 50:1 and 100:1 based on soil total C and total N. Also, any labile C pools in the soil were not taken into consideration when calculating the amount of sucrose to add. However, we assumed that labile C pools would be very low considering that soil OM is ~0.4% in unburned shrub interspaces (E. B. Allen, unpublished data).

The amount of sucrose needed to achieve the two treatment ratios was calculated based on the atomic mass of inorganic N, in the form of NO_3^- and NH_4^+ that was measured from the soil during the end of the summer dry season in 2005. Before the first postfire wet season started, soil samples were taken up to a 5 cm depth in control plots. Three soil cores were pooled per sample and six samples were taken, one for every odd block. Soil cores had a diameter of 2.5 cm. Three larger cores with a diameter of 5 cm were also taken up to 5 cm depth to determine soil bulk density. For bulk density, three blocks were chosen randomly, and only one core per control plot per block was sampled. Sampling was done at the end of each summer dry season and samples were taken to University of California–Riverside for NO_3^- and NH_4^+ analyses on a Technicon Autoanalyzer II continuous flow analyzer (Technicon Instruments, Tarrytown, New York, USA).

Based on bulk density, the amount of inorganic nitrogen (NO_3^- plus NH_4^+) present in the control soils was determined by volume. Then, the amount of sucrose needed to achieve labile 50:1 and 100:1 carbon to nitrogen ratios was determined based on the amount of inorganic nitrogen found per volume of soil and the atomic mass of C in sucrose. For example, to calculate the amount of carbon required to produce a labile 100:1 carbon to nitrogen ratio in the upper 5 cm of soil in a 150×150 cm plot with soil bulk density at $1.27 g/cm^3$ (142 875 g of soil) and inorganic nitrogen levels at 16.1 ppm (2.3 g of inorganic nitrogen), 547.6 g of sucrose was

added to result in an addition of 230 g of carbon, given that 42% of sucrose is carbon by mass. Bulk density, inorganic nitrogen, and the calculated carbon amounts that were applied to 100:1 and 50:1 large plots for each year are listed in Table 1.

For the second and third wet seasons, the same procedure was performed except soils were collected from both the 50:1 and 100:1 plots because inorganic N in the treatment plots had diverged from control levels. The same plots were treated three years in a row to achieve 50:1 and 100:1 labile C:N ratios in the upper 5 cm of soil at the beginning of each wet season. Sucrose was applied once a year in carbon addition plots during or within 24 hours of the first major precipitation event of each wet season. In the second wet season (2006–2007), the first storm was weaker than predicted and supplemental water had to be added to dissolve the sugar into the soil, but the same amount of water was applied to both carbon amendment treatments and to the control plots. However, further storms this season were all weak and no annual plants ever germinated. Soil measures and amounts of sucrose applied in treatments were based on conditions in the top 5 cm of soil. This was done because about 90–95% of propagules are found within this depth (Young and Evans 1975, Guo et al. 1998), many annual species cannot germinate from depths >1 to 2.5 cm (Freas and Kemp 1983, Pake and Venable 1996), and the goal was to reduce soil nitrogen when annuals were germinating and in an early stage of development because the impact to invasive grasses would be greater at this time rather than at a later phenological stage (Beckstead and Augspurger 2004).

Soil and vegetation sampling

Following the first rainstorm of each wet season, additional soil sampling was carried out once a month to once every two months (see Fig. 1) until peak flowering in spring to document soil and microbial responses to the carbon amendments. When soil was sampled after the treatments were implemented during the first rainstorm of the first season (2005-2006), no significant differences in NO_3^-, NH_4^+, and microbial biomass N were found when comparing even vs. odd blocks; thus future soil sampling sessions were reduced to only collect soils from alternating even and odd blocks. Soil sampling consisted of collecting three to four cores at 5 cm depth per plot that were pooled into one sample for analyses. Soils collected during these sampling campaigns were measured for NO_3^-, NH_4^+, and microbial biomass N on a Technicon Autoanalyzer II continuous flow analyzer using a K_2SO_4 extraction solution as described in Sirulnik et al. (2007). In the second season, precipitation was very low and no plants germinated. Thus, soils were only sampled in April, coinciding with the typical period when most native annual plants are in full bloom at the study site.

Throughout the first and third seasons, plant cover was regularly measured from the control treatment from one of the two plots per block. In the second season, no vegetation sampling was performed because no plants germinated. For the first and the third seasons, the first sampling date occurred five days after the first storm in October and December, respectively, and sampling continued in the same plots monthly (excluding March) until peak flowering, which was in April for both seasons. These data were used to track changes in invasive grass, invasive forb, and native annual cover throughout each growing season. For the purposes of this study, peak flowering is defined as the approximately two to three week period in the spring where the highest number of native annual species are in bloom.

At peak flowering in April of both the first and third seasons, several other vegetation parameters were measured but from all three treatments and in all plots. Within plots, a 0.5-m^2 (100 × 50 cm^2) quadrat was used to collect percent cover by species. In the middle of this quadrat, a 0.125-m^2 (50 × 25 cm^2) quadrat was placed to measure density by species (Fig. 2). Plant cover and density were measured from the same permanently marked areas year after year. Biomass was also collected using a 0.125-m^2 quadrat but these samples were harvested outside of the 0.5-m^2 quadrat in an area designated for destructive sampling. Biomass was only collected for three species, the most dominant exotic annual grass (*Schismus barbatus*), exotic annual forb (*Erodium cicutarium*), and native annual forb (*Chaenactis fremontii*). Biomass was never collected from areas that had been previously clipped for biomass or disturbed by soil sampling. Reported biomass values were scaled up to grams per square meter following methods used in Steers and Allen (2009).

Trait measurements

In February 2008, we measured physiological and morphological traits on 11 native (see Appendix A) and three invasive species (*Bromus madritensis*, *Schismus barbatus*, *Erodium cicutarium*) just outside of the sampled plots (*n* = 5–10 individuals per species). We examined physiological (photosynthetic rate, quantum yield, stomatal conductance, water use efficiency, photosynthetic nitrogen use efficiency, leaf N content) and morphological (leaf mass per area, leaf thickness, ratio of root to shoot biomass) traits that capture species differences in the acquisition and use of water and nitrogen. The selected traits were chosen based on (1) their relevance to plant fitness across a soil nitrogen gradient in this arid system (e.g., Chapin 1980, Gulmon and Chu 1981, Reich et al. 1989, Aerts and Chapin 2000, Schwinning and Ehleringer 2001, Westoby et al. 2002) and (2) practicalities in their collection and measurement (e.g., hydraulic traits could not be easily measured on these short-statured annuals with small leaves). Sampling in February allowed us to survey traits near peak plant biomass, just before flowering.

Photosynthetic capacity (*A*, μmol·m^{-2}·s^{-1}), transpiration rates (*E*, mol·m^{-2}·s^{-1}), stomatal conductance (*g*$_s$, mol·m^{-2}·s^{-1}), and chlorophyll fluorescence were measured with a LI-6400 portable photosynthesis system with a fluorescence chamber (LI-COR, Lincoln, Nebraska, USA). All measures were conducted at saturating light levels (1900 μmol photon·m^{-2}·s^{-1}), at 400 μL/L CO$_2$ and under ambient conditions of humidity (40–60%) and temperature (26–28°C). The effective quantum yield of PSII (ΦPSII) was calculated as $(F_{m'} - F_s)/F_{m'}$, where F_s is the fluorescence yield of a light-adapted leaf and $F_{m'}$ is the maximal fluorescence during a saturating light flash. Water use efficiency (WUE) was calculated as the ratio of photosynthesis to transpiration at 1900 μmol photon·m^{-2}·s^{-1}.

Following physiological measurements, we measured leaf thickness with digital calipers. Leaves were then collected, scanned to determine leaf area, dried at 65°C for 3 d, and weighed to determine leaf mass per area (LMA, g/m^2). Leaves were ground to pass a 40 mesh screen and were analyzed for leaf N content with an elemental analyzer (CE Instruments Flash EA 1112; CE Elantech, Lakewood, New Jersey, USA). Photosynthetic nitrogen use efficiency (PNUE) was calculated as the ratio of photosynthesis to leaf N. All physiological and morphological measurements were conducted on recently mature leaves.

All plants were harvested and separated into above- and belowground biomass. To minimize fine root loss, roots were carefully separated from soil and washed. All material was dried and weighed to determine the ratio of root to shoot biomass (R:S).

Data analysis

Soil data included nitrate, ammonium, and microbial biomass N. Vegetation data included cover and density by species, native annual plant species richness, and biomass measures for the most abundant invasive grass, invasive forb, and native annual plant. Cover and density data from the two quadrats per sampling unit were averaged so that *n* = 12 for all vegetation analyses. Soil samples were taken on even or odd plots at each sampling time so *n* = 6 for all soil analyses. Soil and vegetative response to treatments were statistically analyzed using one-way ANOVA with least significant difference (LSD) tests. Data were transformed using arcsine square-root(*x*) for cover, square-root(*x* + 0.5) for density and species richness, and log$_{10}$(*x* + 1) for biomass and soil nutrients when they would improve normality based on goodness-of-fit tests.

Pearson product-moment correlation coefficients were generated to evaluate the linear association between traits and log-transformed percent cover across treatments. Differences in trait values across species were analyzed with ANOVA, and post hoc comparisons were analyzed by Tukey's honestly significant difference. Following Moran (2003), sequential Bonferroni corrections for multiple statistical tests were not conducted. A
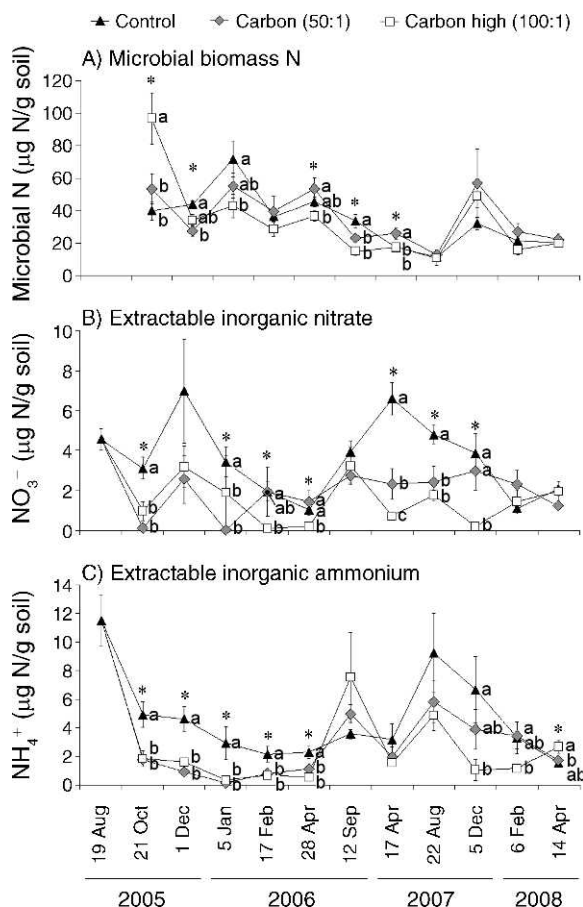
FIG. 3. (A) Soil microbial biomass N, (B) nitrate–N, and (C) ammonium–N for all three treatments (control, and labile C:N ratios of 50:1 and 100:1) throughout the experiment; values are mean ± SE. See Fig. 1 to correspond sampling times with precipitation, carbon addition dates, and season. Asterisks indicate significant differences between treatments per sample time based on ANOVA. Differences in letters between treatments within the same sampling time indicate significant differences based on LSD tests. For some sample times, ANOVA was not significant at $\alpha = 0.05$, while the LSD test was.
* $P < 0.05$.

descriptive multivariate analysis was conducted on standardized trait values using principal components analysis (PCA). Trait data that violated the ANOVA assumptions of normality and homogeneity of variance were Box-Cox transformed. All statistical analyses were performed using JMP 8 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Soils

In general, soil microbial biomass appeared to respond to rainfall, where growth was stimulated by precipitation, specifically the first large storm event after the hot, dry summer, and subsequently contracted, especially in dry periods (Figs. 1 and 3). Between treatments, soil microbial biomass in 100:1 carbon

amended soils usually differed significantly from the control. In general, microbial biomass in 50:1 carbon amended soils paralleled the 100:1 treatment but differed from the control less frequently. However, this was not always the case and at two points during the first season, the carbon amendments differed more from each other while microbial biomass in control plots was in-between the two carbon amendments. At other times, the 50:1 carbon amended soils were more different from the control than the 100:1 amended soils, and sometimes, there were no statistical differences, such as at the end of the third season (Fig. 3). As expected, five days after the first rainstorm of 2005–2006, microbial biomass increased greatly in the 100:1 carbon treatment. Consequently, nitrate (NO_3^-) and ammonium (NH_4^+) were both significantly lower than the control at this time (Fig. 3). Invasive annual grass cover was also significantly lower in 100:1 treated plots compared to control plots at this early-sampling time, and continued to remain lower throughout the rest of the first wet season (R. J. Steers, *unpublished data*).

In general, soil microbial biomass was elevated in carbon amended treatments immediately following the first rain of each season (not measured in second season [2006–2007]). However, when this parameter was measured at other times during each year, microbial biomass was usually lower than the control (Fig. 3), which might be due to contractions during dry periods. For example, besides a small storm that produced <1 mm of precipitation in December of 2005, there was a 72-d period with no precipitation following the first rain of the 2005–2006 wet season (Fig. 1). This drought period seemed to affect soil microbial N in the 100:1 and 50:1 treatments more than in the control. For example, soil microbial N in the 100:1 treatment dropped greatly and persisted at a lower level than the control, often significantly lower for most of the wet season following this drought (Fig. 3).

As expected, soil NO_3^- and NH_4^+ concentration were lower in both carbon amended treatments compared to the control (Fig. 3). This pattern was especially evident during the first season but was also apparent in the beginning of the third season. Soil NO_3^- and NH_4^+ concentration were typically lower in the carbon high (100:1) compared to the carbon (50:1) treatment, but not always. Most importantly, the carbon high treatment was effective at reducing both NO_3^- and NH_4^+ at the beginning of the two growing seasons when precipitation was great enough for annual plants to germinate. Changes to total C and N due to carbon amendments were never detected during this study, with values in control plots of 0.7% ± 0.03% total soil C (mean ± SE) and 0.1% ± 0.00% total N (R. J. Steers, *unpublished data*).

Vegetation

In the first postfire wet season (2005–2006), invasive grasses (mostly *Schismus barbatus*) germinated immedi-
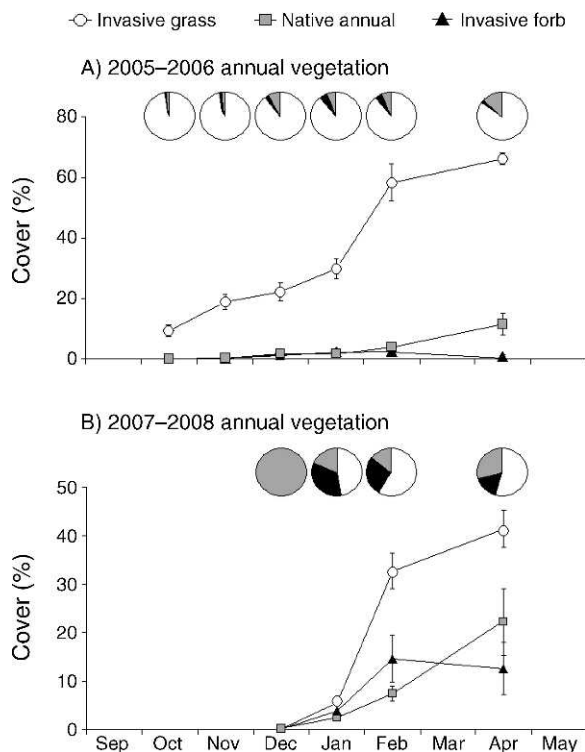
FIG. 4. Line graphs portray the absolute cover (mean ± SE) of invasive grass, invasive forb, and native annuals from control plots throughout the first (2005–2006) and third (2007–2008) wet seasons. Pie charts above points represent the average relative cover of each of the three annual plant categories at respective sampling times.

ately following the first precipitation event and were more abundant than invasive forbs and native annuals during the entire season (Fig. 4). As expected, invasive grass cover, density, and biomass were lower in both

carbon amended plots (50:1 and 100:1) compared to control at the end of the first season (Table 2, Fig. 5). Carbon amended plots did not alter invasive forb cover, density, or biomass in the first season nor native annual plant richness, cover, and biomass (Table 2, Fig. 5). However, because the carbon amendments decreased invasive annual grasses, especially in the high carbon (100:1) treatment, the relative cover of native annuals was greater than in the control treatment (Fig. 6). Likewise, where treatments had reduced invasive grass abundance, cover of bare ground increased greatly (Table 2).

Unlike the first season, in the third postfire wet season (2007–2008) native annuals germinated first and invasive forbs were also relatively abundant at an early point. Other differences in species specific abundance across treatments were also noticeable in this season compared to the first (Appendix B). In the third season, invasive grasses did not dominate until about half-way through the season (Fig. 4). Consequently, invasive and native species in treatments responded differently than in the first season. As expected, invasive grass cover, density, and biomass were again lower in carbon amended plots compared to control. However, several measures of invasive forb and native annual abundance were also lower in carbon amended soils (Table 2, Fig. 5). Unlike the first season, invasive forb cover was lower in the 100:1 amended plots compared to control (Fig. 5) and invasive forb biomass was lower in both carbon amended plots compared to control (Table 2). Native annual plants were also negatively affected by the carbon amendments in the third season. Native richness, cover, density, and biomass were all lower in both carbon amended plots compared to control (Table 2, Fig. 5). Because carbon amendments reduced all plant groups in the third season (Fig. 5), relative cover and

TABLE 2. Average vegetation and soil parameters by treatment (control, and labile C:N ratios of 50:1 and 100:1) and year measured at the end of each wet season (April).

	Control		Carbon (50:1)		High carbon (100:1)	
Parameter	2006	2008	2006	2008	2006	2008
Native richness (no. spp./0.5 m^2)	3.5	5.9^a	3.8	4.2^b	3.1	4.7^{ab}
Density (no./m^2)						
Invasive grass	1628^A	3179^a	1405^{AB}	1764^b	969^B	1600^b
Invasive forb	4	44	5.6	32.8	4.8	26.4
Native	41.6^{AB}	232	80.8^A	123.2	19.2^B	89.6
Relative density (%)						
Invasive grass	96	91.6	91.1	90.6	97	92.7
Invasive forb	0.3	1.5	0.6	2.3	0.5	1.6
Native	3.8	7	8.3	7.2	2.6	5.7
Biomass (g/m^2)						
Schismus	125.5^A	118^a	24^B	23.5^b	19.2^B	13.6^b
Erodium	4.3	14.1^a	5.6	2.4^b	7.3	1.9^b
Chaenactis	18.5	74.2^a	21.9	10.9^b	15	11.9^b
Bare ground cover (%)	29.5^A	25.3^a	54.3^B	73.6^b	60.9^B	75.8^b

Notes: Different superscript letters indicate significant differences between treatments within years, based on LSD tests. Uppercase superscripts are used for 2006, and lowercase for 2008.
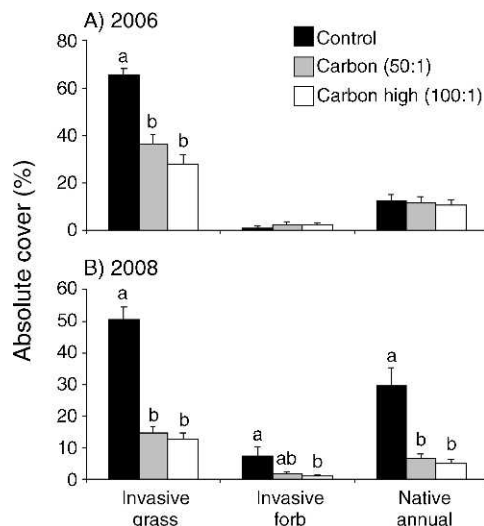
FIG. 5. Absolute cover (mean + SE) of annual vegetation: invasive grass, invasive forb, and native annuals at end of the wet season (April) by treatment in the (A) first and (B) third year. If significant differences between treatments for each species group exist, they are indicated by different letters. Differences were determined based on ANOVA and LSD tests at $\alpha = 0.05$.

relative density of invasive annual grasses, forbs, and native annuals were not different between treatments (Table 2, Fig. 6).

Trait data

A PCA was conducted using traits that reflect water and nitrogen use (Fig. 7). Axis 1 separated species based on carbon assimilation (A, $\Phi PSII$, PNUE). Axis 2 was associated with water use (R:S, WUE). Overall, the two axes explained 57.8% of the variance among species. The three invasive species (*Bromus madritensis* ssp. *rubens*, *Schismus barbatus*, *Erodium cicutarium*) had lower photosynthetic function than many native species (Fig. 7). Relative to all other species, *S. barbatus* had thin leaves, low LMA, and low leaf N content (Appendix A). *Bromus madritensis* had relatively low leaf N content and very low PNUE (Appendix A).

Few traits significantly correlated with percent cover (Table 3). In 2006 and 2008, the efficiency of Photosystem II ($\Phi PSII$), a measure of light-use efficiency, was negatively correlated with percent cover in most treatments. In 2006, LMA was negatively correlated with percent cover in the control treatment. When *S. barbatus*, which had the highest percent cover in both the first and third seasons, was excluded from the analysis, WUE was strongly correlated with percent cover in all three treatments in both years (*data not shown*). Nitrogen-use traits (leaf N content, PNUE) did not correlate with percent cover in any treatment, even when *S. barbatus* was removed from the analysis.

In the first season (2005–2006), plant species that were less adversely affected by carbon amendments (positive

or small decrease in percent cover in the 50:1 treatment relative to control) had high LMA and WUE (Fig. 8). In the third season (2007–2008), species with high leaf N content displayed smaller reductions in percent cover in the 50:1 treatment relative to the control (Fig. 8); however, this pattern was driven by the legume *Lupinus bicolor*.

DISCUSSION

Do traits predict the success of resource manipulation?

We hypothesized that carbon amendments would reduce invader biomass based on previous work that demonstrated invasive species are more nitrophilous than native species. In contrast, two of the three invasive species examined (*Bromus madritensis*, *Schismus barbatus*) had low N content. This suggests that they did not require large amounts of N, or were less sensitive to changes in N availability, which supports results from another study of *B. madritensis* (DeFalco et al. 2003). Thus, our second hypothesis that carbon amendments will disproportionately decrease the performance of exotic annual grasses does not follow. Nevertheless, compared to *Erodium cicutarium* and native forbs, we did observe a large relative decrease in exotic annual grass cover, density, and biomass in response to carbon
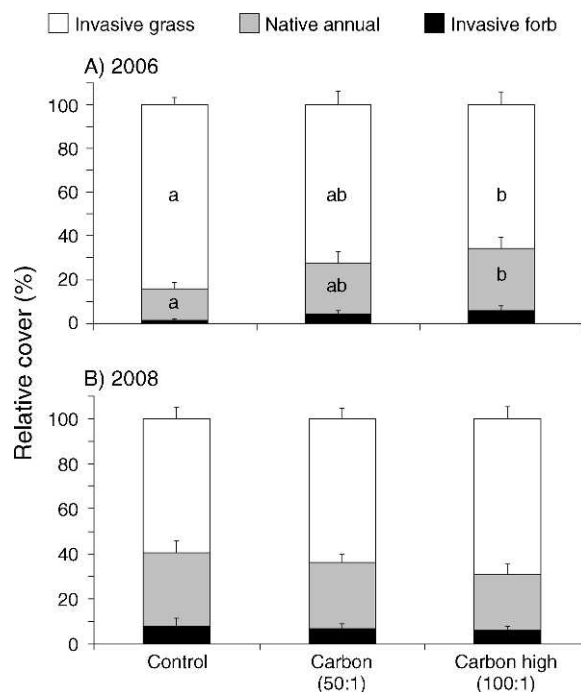

FIG. 6. Relative cover (mean + SE) of annual vegetation: invasive grass, invasive forb, and native annuals at the end of the wet season (April) by treatment in the (A) first and (B) third year. If significant differences between treatments for each species group exist, they are indicated by different letters. Differences were determined based on ANOVA and LSD tests at $\alpha = 0.05$.
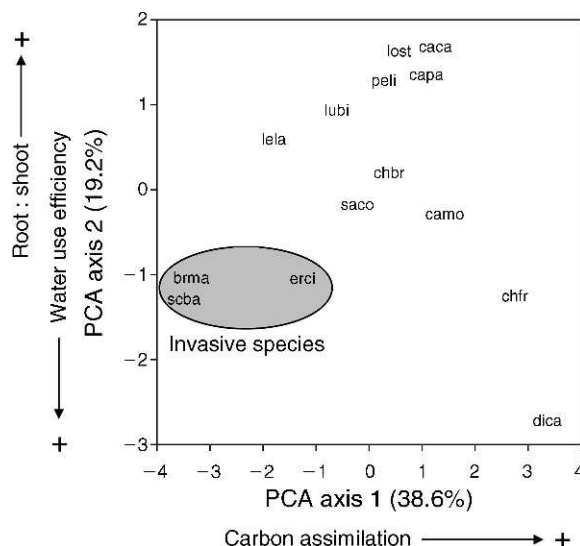
FIG. 7. PCA results for functional traits from three invasive and 11 native species. Carbon assimilation (A_{max}, ΦPSII, PNUE) and water use (R:S, WUE) traits accounted for 38.6% and 19.2%, respectively, of the variation among species; ΦPSII is the effective quantum yield of Photosystem II, WUE is water use efficiency, and PNUE is photosynthetic nitrogen use efficiency. The three invasive species clustered together primarily based on low photosynthetic function, but *Bromus madritensis* (brma) and *Schismus barbatus* (scba) had low R:S and moderately low WUE. Other species abbreviations are as follows: *Dichelostemma capitatum* (dica), *Chaenactis fremontii* (chfr), *Erodium cicutarium* (erci), *Pectocarya linearis* (peli), *Camissonia pallida* (capa), *Lupinus bicolor* (lubi), *Lepidium lasiocarpum* (lela), *Lotus strigosus* (lost), *Camissonia californica* (caca), *Salvia columbariae* (saco), *Calyptridium monandrum* (camo), and *Chorizanthe brevicornu* (chbr).

amendments in the first season. In the third season, exotic annual grasses were again impacted, but so were all other species groups. Therefore, traits other than N-use such as WUE and germination timing may determine the success of desert annuals in resource manipulation contexts.

While *S. barbatus* was adversely affected by carbon amendments, some plant species were not as severely impacted by this manipulation. In the first season, species with high LMA and WUE had higher percent cover in 50:1 plots relative to control plots. Plant species occurring in arid regions can increase WUE by investing more resources in the photosynthetic machinery located in the mesophyll cells to draw down intercellular CO_2 concentrations and reduce transpiration loss (Westoby et al. 2002). Larger amounts of mesophyll tissue and photosynthetic enzymes can result in increased LMA and N, respectively (Wright and Westoby 2002). The positive association of LMA and WUE with the change in percent cover between the control and 50:1 treatment suggests that water-use traits contributed to plant success in the 50:1 carbon treatment. However, in the third season, species with high leaf N content were less adversely affected by carbon amendments (i.e., lower cover in 50:1 plots relative to control plots). This was driven primarily by high percent cover of the legume *L. bicolor* in the 50:1 carbon treatment. When *L. bicolor* is excluded from the analysis, our data support the idea that traits associated with water use, as opposed to N use, strongly influence plant performance in this system.

Overall, these trait data suggest that carbon amendments will not disproportionately impact invasive annuals since they do not have higher N requirements. Because many native annuals require high leaf N content to maintain high WUE, carbon amendment treatments should adversely affect native annuals, and this was evident in the third season when native annuals emerged first. For example, *Chaenactis* biomass and density declined in both 50:1 and 100:1 treatments during the third season. Thus, our data suggest that the most effective restoration strategy may be to manipulate water availability, although we are aware of no such large-scale water manipulation treatments. However, desert precipitation displays high interannual variation (Hereford et al. 2006), and this may help native annual

TABLE 3. Pearson's correlation coefficients (r) for the relationships between plant traits and percent cover at the species level in three treatments (control and labile C:N ratios of 50:1 and 100:1) in 2006 and 2008.

	2006			2008		
Trait	Control	50 C:N	100 C:N	Control	50 C:N	100 C:N
Leaf thickness	−0.24	−0.25	−0.16	−0.09	−0.07	−0.06
LMA	−0.52*	−0.42	−0.37	−0.35	−0.34	−0.32
Root : shoot ratio	−0.10	−0.09	−0.09	−0.20	−0.24	−0.24
Photosynthetic rate	−0.42	−0.43	−0.38	−0.23	−0.19	−0.17
Stomatal conductance	−0.32	−0.36	−0.38	−0.21	−0.40	−0.41
ΦPSII	−0.53*	−0.58*	−0.58*	−0.43	−0.57*	−0.55*
WUE	0.00	0.11	0.17	0.28	0.38	0.37
Leaf N (mass)	−0.28	−0.30	−0.29	−0.23	−0.25	−0.29
Leaf N (area)	−0.38	−0.39	−0.42	−0.40	−0.37	−0.40
PNUE	−0.18	−0.20	−0.13	0.01	0.01	0.04

Notes: LMA is leaf mass per area, ΦPSII is the effective quantum yield of Photosystem II, WUE is water use efficiency, and PNUE is photosynthetic nitrogen use efficiency. We sampled 14 species. Significant correlations are indicated.
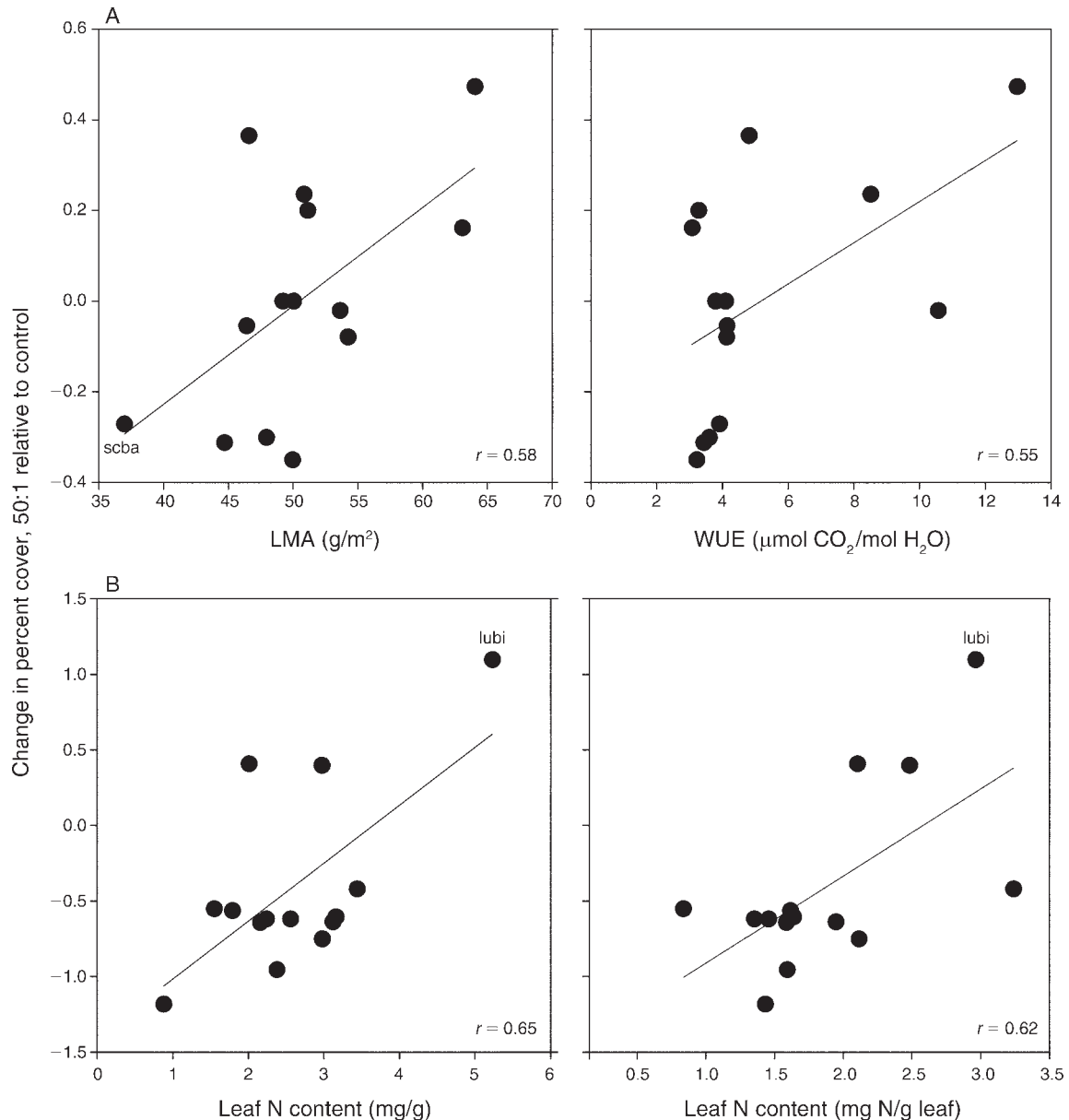* $P < 0.05$.

FIG. 8. Correlations between traits and change in percent cover of species between the low carbon-addition (50:1) treatment and the control at the end of the (A) first and (B) third seasons. For the first season, LMA (leaf mass per area) and WUE were correlated with change in percent cover while in the third season, leaf N content on an area and mass basis were correlated. The outliers *Schismus barbatus* (scba) and *Lupinus bicolor* (lubi) are noted in the figure. Pearson's correlation coefficients (r) for the relationships are provided ($P < 0.05$).

persistence (Levine and Rees 2004) as invasive species die back in dry years (Salo 2004, Minnich 2008).

Efficacy of carbon amendment

In the first and third wet seasons, carbon amendments reduced exotic annual grasses as hypothesized. However, native annuals were also affected by carbon amendments in the third season, which we did not expect a priori. Also, *Erodium cicutarium*, the only exotic annual forb, was also impacted in the third season only

(see Plate 1 and Appendix C). Besides physiological differences, there may be other factors that can explain why carbon amended soils worked as predicted in the first season but not in the third. In the first season, invasive annual grasses, especially *Schismus barbatus*, were abundant immediately following the first rains. Consequently, invasive grasses were disproportionately impacted by the carbon amendments. In the third season, instead of invasive grasses dominating the early stages of the herbaceous community, native annuals

PLATE 1. Small-sized annual forbs, like the exotic species *Erodium cicutarium* (redstem filaree) shown here, were especially characteristic of sucrose-amended soils in 2008. A color version of this photo is available in Appendix C. Photo credit: R. J. Steers.

were the first species to germinate and were especially abundant. *Erodium cicutarium* was also relatively common early in the third season. Consequently, native annuals and *E. cicutarium* were highly impacted by the carbon amendment treatments this season. Therefore, carbon amendments that lower inorganic soil N can negatively impact both invasive and native species of this desert environment. Whichever species group is more impacted will largely depend on which one is relatively more abundant when N is immobilized (Corbin and D'Antonio 2004). Similarly, N additions have been shown to increase both invasive grasses and native annuals, depending on which species group is more abundant (Allen et al. 2009). Because this treatment was focused on impacting species at germination and early stages of development, our results may have differed had we applied the amendments later in the season.

In accordance with other desert studies (Gallardo and Schlesinger 1995, Schaeffer et al. 2003), labile carbon amendments (i.e., sucrose) effectively lowered inorganic pools of N at our study site, at least during the beginning of the wet season following application. At the beginning of the first season, microbial biomass was elevated in carbon amended plots while soil inorganic nitrogen was low, which was the expected response (Zink and Allen 1998, Alpert and Maron 2000). Although after this point, microbial biomass dropped and was often significantly lower than the control throughout the experiment, while inorganic nitrogen in carbon amended plots was also lower for much of the remaining study period, at least for the 100:1 treatment. This unexpected disconnect between microbial biomass N and inorganic N has not been noted elsewhere to our knowledge. However, Bleier and Jackson (2007) found a disconnect between inorganic N supply and plant response while utilizing sawdust and sucrose amendments. In our study, it is possible that a large amount of microbial biomass lysed during the dry period that immediately followed the first rainstorm of the 2006 season (Van Gestel et al. 1992), while inorganic nitrogen was kept low possibly from nitrification and/or from leaching below 5 cm depth once the rains resumed. In the third season, the carbon high (100:1) treatment was only effective at lowering inorganic nitrogen at the beginning of the season. Among all treatments, as

inorganic nitrogen became less abundant during the third season, the low sample size may have been inadequate to detect meaningful differences in soil parameters between treatments. In summary, despite a short duration of nitrogen immobilization in amended soils, when synchronized with the first rainstorm of the growing season, carbon amendments were capable of reducing exotic annual grass abundance throughout an entire growing season but also had nontarget effects when natives germinated early.

Conclusion

There are several drawbacks of using carbon amendments to control invasive grasses in desert ecosystems. First, the effect of sucrose is not long-lasting (Reever Morghan and Seastedt 1999, Alpert 2010), and invasive grasses are expected to regain dominance once the carbon amendment is mineralized. Second, the cost of applying sucrose over large areas may be prohibitive (Alpert and Maron 2000). Third, high interannual variability in rainfall and species composition of annual plants in desert ecosystems (Freas and Kemp 1983, Philippi 1993, Pake and Venable 1996) can make early-season applications a waste of effort due to lack of rainfall (e.g., second season) or counterproductive when native annuals germinate early and are negatively impacted (e.g., third season). Among these drawbacks are a number of other pitfalls (reviewed in Alpert 2010 and Perry et al. 2010). However, some of the negative attributes of carbon amendments could be overcome by developing an understanding for how much carbon to apply, understanding timing of application, and by incorporating knowledge of plant species traits.

While most of the annual species in this study appear to be impacted by low N conditions, the early germination and rapid phenology that is typically exhibited by invasive annuals in this system makes them especially susceptible to carbon additions at the beginning of the growing season. With respect to N manipulation, N-use traits such as those measured in this study do not correlate with the success of species in this desert system because both invasives and natives differ little in this regard. We observed that when exotic annuals are more abundant early in the season they are highly impacted by low soil N, and when native annuals are more abundant early in the season then they are highly impacted. However, invasive grasses have lower water use efficiency and consequently, would be more susceptible to drought, which is supported by field observations (Salo 2004, Minnich 2008; see *Results*). While large-scale water manipulations that reduce invasive grasses are not feasible, early-season carbon amendments do have the potential to be successful under ideal conditions. Nevertheless, carbon amendments are not expected to perform as well as other contemporary invasive species control methods like herbicides. For example, the grass-specific herbicide Fusilade II not only kills both invasive annual grasses

(*Schismus* spp. and *Bromus madritensis*) and forbs (*E. cicutarium*), it also significantly increases native annual abundance and species richness (Steers and Allen 2009), which the early-season carbon amendments were never able to do in this study. For this reason and those mentioned previously, carbon amendments remain a relatively less optimal tool for invasive annual species control in desert environments. However, in situations where invasive species differ strongly in N-use traits compared to desired species, use of carbon amendments may be very successful.

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APPENDIX A

Resource-use traits measured for 14 species at Big Morongo Canyon Preserve, California, USA (*Ecological Archives* A021-055-A1).

APPENDIX B

Average cover of species found in experimental plots in 2006 and 2008 (*Ecological Archives* A021-055-A2).

APPENDIX C

A color version of Plate 1 (*Ecological Archives* A021-055-A3).