

Simple plant traits explain functional group diversity decline in novel grassland communities of Texas

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Abstract Previous research has found that plant diversity declines more quickly in exotic than native grassland plots, which offers a model system for testing whether diversity decline is associated with specific plant traits. In a common garden experiment in the Southern Great Plains in central Texas, USA, we studied monocultures and 9-species mixtures of either all exotic or all native grassland species. A total of 36 native and exotic species were paired by phylogeny and functional group. We used community-level measures (relative abundance in mixture) and whole-plant (height, aboveground biomass, and light capture) and leaf-level traits (area, specific leaf area, and C:N ratio) to determine whether trait differences explained native-exotic differences in functional group diversity. Increases in species' relative abundance in mixture were correlated with high biomass, height, and light capture in both native and exotic communities.

However, increasing exotic species were all C₄ grasses, whereas, increasing native species included forb, C₃ grass and C₄ grass species. Exotic C₄ grasses had traits associated with relatively high resource capture: greater leaf area, specific leaf area, height, biomass, and light capture, but similar leaf C:N ratios compared to native C₄ grasses. Leaf C:N was consistently higher for native than exotic C₃ species, implying that resource use efficiency was greater in natives than exotics. Our results suggest that functional diversity will differ between grasslands restored to native assemblages and those dominated by novel collections of exotic species, and that simple plant traits can help to explain diversity decline.

Keywords Novel ecosystems · Biodiversity · Invasive species · Altered rainfall · Functional diversity · *Eragrostis curvula* · *Panicum coloratum* · *Sorghum halepense*

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Introduction

Exotic (non-native, alien) species have become common and even dominant in grassland ecosystems throughout North America (Christian and Wilson 1999; Callaway and Aschehoug 2000; Cully et al. 2002; Seabloom et al. 2003; Corbin and D'Antonio 2004; Gendron and Wilson 2007). Native grasslands have been converted to exotic-dominated ecosystems either by intentional plantings of exotics or by exotics

displacing natives (Wilsey et al. 2009). Exotic grasslands can persist for many years even when native seed sources are nearby (e.g., Christian and Wilson 1999; Wilsey and Polley 2003; Kulmatiski 2006). Observational and experimental studies in the Great Plains have found that species diversity at the site-level declines as exotic communities replace native ones in modern landscapes (e.g., Christian and Wilson 1999; Wilsey et al. 2011; Isbell and Wilsey 2011b), a result that is in contrast with the increased diversities associated with invasions of remote-island forested systems (Mascaro et al. 2012), but consistent with the view that dominant exotic plant species possess traits that separate them ecologically from natives. For example, Firm et al. (2011) found that grasses were more abundant and forbs were less abundant in their introduced ranges than their home ranges, suggesting that there are important ecological differences between exotic grasses and forbs. In three common garden experiments, we have found differences between native and exotic species and communities in both the northern and southern Plains of the United States (Wilsey et al. 2009, 2011; Isbell and Wilsey 2011a, b). For example, Wilsey et al. (2009) reported that native communities had 46 and 35 % higher species diversity and richness than did exotic communities. Simple traits or trait matrices (McGill et al. 2006) potentially could be used to predict these declines in diversity.

Native communities often have higher species and functional group diversity than exotic communities (Christian and Wilson 1999; observational results of Wilsey et al. 2011). However, because exotics usually establish under disturbed conditions where resource availability tends to be higher, it is difficult to determine if the exotics themselves are causing diversity decline (i.e., are drivers), or if exotics are associated with conditions such as disturbance and high resource availability that reduce diversity (i.e., are passengers, Seabloom et al. 2003; MacDougall and Turkington 2005; Hille Ris Lambers et al. 2010; Price et al. 2011). A meta-analysis of trait differences between native and non-native species showed that non-natives tend to have traits that are associated with rapid aboveground growth (Leishman et al. 2007). However, differences in trait values between invaded and non-invaded areas could be partially or even solely due to differences in resource availability or other environmental factors rather than differences in the species themselves. As Vilà and Weiner (2004)

point out, many of the previous comparisons of natives and exotics were at least partially confounded by other differences (e.g., they compared annuals to perennials, or plants in disturbed areas to plants in less disturbed areas). Common garden studies, whether done in the greenhouse (MacDougall and Turkington 2005; Badgery et al. 2005; Firm et al. 2011) or in the field (this study), offer an important complementary approach. By comparing species in a common environment, we can test for differences that are independent of other covarying factors. Here, we take this approach to determine whether trait differences between natives and exotics explained native-exotic differences in functional group and species diversity decline.

The MEND (maintenance of exotic vs. native diversity) project was established in 2007 and 2008 in central Texas to compare species diversity decline between all exotic and all native grassland communities grown in common garden conditions (Wilsey et al. 2009). Exotic species chosen for the study were paired by phylogeny and growth form with native species, which is necessary to test for true differences (i.e., with no confounding factors) between native and exotic species. The MEND Phase II study uses monocultures and 9-species mixtures to compare yielding behavior and any associated diversity declines between native and exotic communities under summer irrigated and control conditions (Wilsey et al. 2011). Here, we compare plant traits of the 36 exotic and native perennial species (18 pairs) used in the MEND Phase II study. In the gulf states of the United States, it has been predicted that global change will lead to an increased frequency of tropical storms bringing more precipitation in the summer months that are typically dry (Allan and Soden 2008). Therefore, we tested the impact of increased precipitation during summer on exotic and native species. Dukes and Mooney (1999) predict that exotic species will be more successful than native species in the face of global change particularly when conditions change to become more like those in exotic species' native range (Hellmann et al. 2008). Species that were paired by phylogeny and growth form were grown under ambient conditions and with summer irrigation to test the overall question of whether exotics and natives differ consistently in plant traits across all the grassland functional groups of C₄ grasses, C₃ grasses, forbs, and legumes versus an alternative idea that exotic-native differences are more pronounced in

some functional groups than others. These functional groups delineate major physiological (i.e., mode of photosynthesis in grasses, ability to harbor nitrogen fixing bacteria in legumes) and ecological differences associated with phylogenetic groups (e.g., broad-leaved dicotyledonous forbs vs. monocotyledonous grasses) in tallgrass prairie systems (Kindscher and Wells 1995). In particular, we hypothesized that (1) trait differences between natives and exotics would explain differences in relative abundances and functional group diversity between native and exotic communities, (2) trait differences would be greater in the functional group that becomes dominant (C_4 grasses in this case) than for subordinate groups (C_3 grasses and forbs), (3) trait differences between natives and exotics would explain the differing responses of functional groups to summer irrigation. Since large differences in diversity and interspecific interactions were previously found between natives and exotics in this study (Wilsey et al. 2011), we test whether plant traits correlate with the success of the functional groups that increase in mixture.

Methods

Study site

The experiment was conducted on lands owned by the USDA-ARS Grassland, Soil, and Water Research Lab in Temple, Texas within the Blackland prairie region (Wilsey and Polley 2003, 2006). The experiment was established on a field that was cropped in the early part of the 20th century and then used for occasional bouts of cattle grazing thereafter. The field was dominated by the exotic C_4 grass *Bothriochloa ischaemum* before the experiment was established. Nearby native prairie remnants are quite diverse and contain a great number of grass, forb, and legume species (Polley et al. 2005). Exotic grasslands in the area are dominated by C_4 grasses (Wilsey et al. 2011). Soils are Vertisol usterts.

Experimental design

The experiment was designed as a 2-way factorial (irrigation \times origin) in a randomized block design, with species pairs (exotic/native) for monocultures and draws for mixtures nested within spatiotemporal blocks. There were two blocks representing two

planting times, October 2007 and March 2008. Two planting times were used to allow for broader inferences and to prevent certain species or functional groups from being favored by planting time. To establish the experimental plots, the study area was treated with glyphosate herbicide to remove the *B. ischaemum* and was then disked. Afterward, new *B. ischaemum* seedlings were weeded during the first year from all plots. The design involved planting roughly equal-mass (mean of 0.7 g/plant) transplants of 18 exotic and 18 native perennial species found in the region (Diggs et al. 1999; Polley et al. 2005) paired by phylogeny, growth form, and mode of photosynthesis (Table 1). Plots were planted with either all exotic or all native species in either monoculture or 9-species mixtures. Only exotics that were already present in the region were used, and no new exotic species were introduced. We used a total of 12 C_3 species pairs, of which only two were C_3 grass species due to their paucity in the region. Exotic and native species were paired in such a way that the phylogenetic distances between individual species in exotic communities were approximately the same as the phylogenetic distances in the native communities (Cadotte et al. 2008). Each block included 32 mixtures and 72 monocultures. Thus, there were 144 monoculture plots (18 species \times 2 origins [native or exotic] \times 2 irrigation treatments \times 2 blocks), and 64 mixture plots (4 draws \times 2 origins \times 2 irrigation treatments \times 2 replicates \times 2 blocks) in total.

The plants used in the study came from seed or vegetative propagules that were either hand-collected or purchased from local seed companies (Wilsey et al. 2011). All the natives used were local genotypes. Equal-mass seedlings were grown in field soil in greenhouses and then were transplanted to the study site and planted in 1 m² plots at a controlled density of 72 seedlings per plot (Wilsey et al. 2011). Relative abundances in mixtures were based on previous work in the area (Wilsey and Polley 2003), which allowed us to plant mixtures that had realistic species diversities and relative abundances. In each mixture plot, we planted ten of each of four C_4 grass species, eight plants of one C_3 grass species, and six plants each of four forb species (three non-leguminous and one leguminous forb). The species used for the mixtures were randomly drawn from our native-exotic species pool, with draws being done so that exotic-native pairs were always selected together to avoid the

Table 1 The perennial exotic and native species that were compared in this study, which were paired by phylogeny, growth form, and mode of photosynthesis

Exotic	Taxon shared	Origin of exotic	Paired native
C₄ grasses			
<i>Bothriochloa ischaemum</i>	Tribe Andropogoneae	Asia	<i>Schizachyrium scoparium</i>
<i>Cynodon dactylon</i>	Tribe Cynodonteae	Africa	<i>Buchloe dactyloides</i>
<i>Eragrostis curvula</i>	Tribe Eragrostideae	Africa	<i>Sporobolus asper</i>
<i>Panicum coloratum</i>	Genus <i>Panicum</i>	Africa	<i>Panicum virgatum</i>
<i>Paspalum dilatatum</i>	Tribe Paniceae	South America	<i>Eriochloa sericea</i>
<i>Sorghum halepense</i>	Tribe Andropogoneae	Mediterranean	<i>Sorghastrum nutans</i>
C₃ grasses			
<i>Dactylis glomerata</i>	Subfamily Pooideae	Eurasia	<i>Nassella luecotricha</i>
<i>Festuca arundinacea</i>	Subfamily Pooideae	Europe	<i>Elymus canadensis</i>
Forbs			
<i>Leucanthemum vulgare</i>	Asteraceae	Eurasia	<i>Ratibida columnifera</i>
<i>Taraxacum officinale</i>	Asteraceae	Europe	<i>Marshallia caespitosa</i>
<i>Cichorium intybus</i>	Asteraceae	Eurasia	<i>Vernonia baldwinii</i>
<i>Nepeta cataria</i>	Lamiaceae	Eurasia	<i>Salvia azurea</i>
<i>Ruellia britoniana</i>	Genus <i>Ruellia</i>	Mexico	<i>Ruellia humilis</i>
<i>Marrubium vulgare</i>	Lamiaceae	Eurasia, Mediterranean	<i>Monarda fistulosa</i>
Legumes			
<i>Lotus corniculatus</i>	Fabaceae	Eurasia	<i>Desmanthus illinoensis</i>
<i>Trifolium repens</i>	Subfamily Papilionoideae	Europe	<i>Dalea candidum</i>
<i>Medicago sativa</i>	Subfamily Papilionoideae	Eurasia	<i>Dalea purpurea</i>
<i>Coronilla varia</i>	Subfamily Papilionoideae	Europe, Mediterranean	<i>Astragalus canadensis</i>

All of the selected species are found in the Blackland Prairie region (Diggs et al. 1999)

confounding effects of life form and phylogenetic differences (Smith and Knapp 2001; Agrawal and Kotanen 2003). Thus, all functional groups were present in each plot at planting. There were 2-m alleyways between each plot, which were seeded with *Bouteloua curtipendula*. Transplanted seedlings were watered during the first 2 weeks to insure establishment. Throughout the study, plots were weeded by removing volunteer seedlings when very small.

Summer irrigation treatments

The region has long growing seasons and a strong bimodal precipitation pattern with a large peak in precipitation in spring, a smaller peak in the fall, and relatively dry summers (July and August). The irrigated plots received a total of 128 mm of water from mid-July to mid-August when water is most limiting (Wilsey et al. 2011). This irrigation pattern

also lessens the magnitude of the typical bimodal precipitation pattern. The irrigation quantities were chosen to match those very infrequent years with especially rainy summer months based on the precipitation records at the site. Based on this, we irrigated twice weekly at a rate of 128 mm/month in eight events of 16 mm between July 15 and August 15. In 2008, rainfall was close to average for the region by July (570 mm) so summer irrigation increased precipitation by 23 % (698 mm). Irrigated plots were watered with a spray nozzle attached to a wand with a flow meter. Water was applied at a rate that eliminated run off. Soil moisture was compared between randomly chosen irrigated and non-irrigated plots, and results were reported by Wilsey et al. 2011. Gravimetric soil water content to 5 cm depth was significantly greater in irrigated than non-irrigated plots and differences were found at all depths sampled (0–45 cm depth) (Wilsey et al. 2011).

Community responses

We estimated abundance of functional groups because of their importance to functional diversity (e.g., Hooper and Dukes 2004; Hille Ris Lambers et al. 2004), and because diversity decline in this system is typically associated with the C_4 grass functional group (Wilsey et al. 2011). Biomass was clipped at 2 cm in October 2008, separated by species, dried at 65 degrees C in a dryer for 48 h and weighed. We estimated functional group diversity and species relative abundances (biomass of each species/total) from these biomass data for each mixture plot. Simpson's diversity index ($1/\sum p_i^2$) was used to calculate functional group diversity, where p_i is the proportion of each functional group (C_4 and C_3 grasses, forbs, legumes). This measured primarily the evenness of functional group biomass because few plots had missing functional groups and all were planted with all four functional groups. This measure is one of the simplest measures of functional diversity (Schleuter et al. 2010), and it is appropriate for grassland systems like this one with well-defined functional groups.

Point intercept techniques were used to determine biomass, species composition, and species diversity of all the plots in the second growing season (June 2009). In this region, biomass production peaks in late June for C_3 species and in late October for C_4 species (Wilsey et al. 2011). During the dry summer months, species can go dormant and senescence can cause a decrease in total biomass and species height in C_3 species. For this reason, we measured biomass and species composition during both June and October (Wilsey et al. 2011). We vertically dropped pins 25 times in the inner 80 × 80 cm portion of each plot and recorded all plant contacts with the pins. Species not hit but present were given a value of 0.5 hits. Point intercept data were converted to biomass with regression equations based on concurrent biomass harvests and point intercept sampling done in October 2008 (Wilsey et al. 2011). Relationships between species number of hits and biomass were strongly linear (mean r^2 across 35 species was 0.89 with a range of 0.69–0.99; *Trifolium repens*, which went locally extinct after the first growing season was excluded).

Whole-plant and leaf-level traits

Whole-plant traits (height, biomass, light capture) and leaf-level traits (leaf area, specific leaf area, C:N ratio)

were measured on species growing in monoculture (Gaudet and Keddy 1988; Shipley et al. 2006; Zhou et al. 2007). Biomass was based on the October 2008 harvest, and because the transplants had roughly equal biomass at planting, is a measure of growth rates. Species heights were determined in June and October by the point intercept method, in which a metal rod with 10 cm increments marked on it was dropped from a frame at a height of 100 cm from the ground in 25 random points in each monoculture. All plant hits were recorded. The two tallest points of interception per species were averaged to represent plant height. In a few cases, the plants grew above 1 m, so the pin was raised above the frame to measure the height. Mean light capture was estimated monthly by measuring the photosynthetically active radiation (PAR) above and below the canopy at the soil surface with an AccuPAR LP-80 ceptometer light bar. Two readings were taken below the canopy at opposite angles and averaged. Percentage light capture was calculated as: $LC = 1 - (\text{mean } PAR_{\text{below}}/PAR_{\text{above}})$.

Leaf-level traits were estimated from two leaves (a first fully-expanded leaf taken from two separate plants) that were randomly selected from each plot and clipped at the base of the petiole in June 2008. Values from the two plants were averaged for each plot to avoid pseudoreplication. In cases where the species had compound leaves, the entire compound leaf was sampled. The leaves were immediately scanned using a Licor leaf area meter. The leaves were dried for 48 h and then weighed to determine specific leaf area (SLA = leaf area/leaf mass). The dried leaves were finely chopped with scissors and analyzed with a C:N analyzer (an Elementar vario Max CN analyzer for samples >10 mg and a Fisons NA 1500 NCS for samples <10 mg) for leaf N and C content. Comparisons between samples that were either chopped or ground were not significantly different (Wilsey unpublished data). Standards were run on both analyzers and compared to insure that there was no machine bias in the data.

Statistical analyses

A mixed model ANOVA was used to analyze community variables, with draw (block) and its interactions treated as random terms and irrigation and origin treated as fixed terms using PROC MIXED of SAS (Littell et al. 2002). The relative abundances of

the four functional groups were interdependent, so MANOVA was conducted, using PROC GLM. When origin and origin \times draw (block) were significant in the MANOVA, the variables were then analyzed with ANOVA. *A priori* contrasts were made of species within functional groups (C_4 and C_3 grasses, forbs, and legumes) to compare how native and exotic functional groups differed.

The trait data derived from the species monocultures (leaf area, specific leaf area, leaf C:N ratio, peak species height, biomass, peak light capture, and the change in height, biomass and peak light capture with irrigation) were analyzed with multivariate ANOVA (MANOVA) using PROC GLM of SAS (Littell et al. 2002). Species (pair) was considered as a random term. An initial analysis with response to irrigation (difference between irrigated and non-irrigated plots) and means of traits across irrigation treatments ($n = 72$) found that irrigation effects were minimal and did not significantly interact with origin. Therefore, we present the full dataset ($n = 144$) that excludes responses to irrigation. The ANOVA's were then considered because the species \times pair interaction in the MANOVA was always significant. To minimize heteroscedasticity, leaf area and biomass were $\log(Y + 1)$ transformed. *A priori* contrasts were made of origin differences within each functional group to test whether native and exotic functional groups differed.

To test for relationships between plant traits and species performance in mixture, we performed a principal components analysis and then tested for relationships between change in relative abundance in mixture and PCA loadings. PCA was used rather than multiple regression on individual variables due to intercorrelation among variables. Principal component loadings were then regressed against change in relative abundance from planting to the end of the first growing season in mixture with stepwise multiple regression techniques for all plots together, and then separately for native and exotic communities. All analyses were done with SAS.

Results

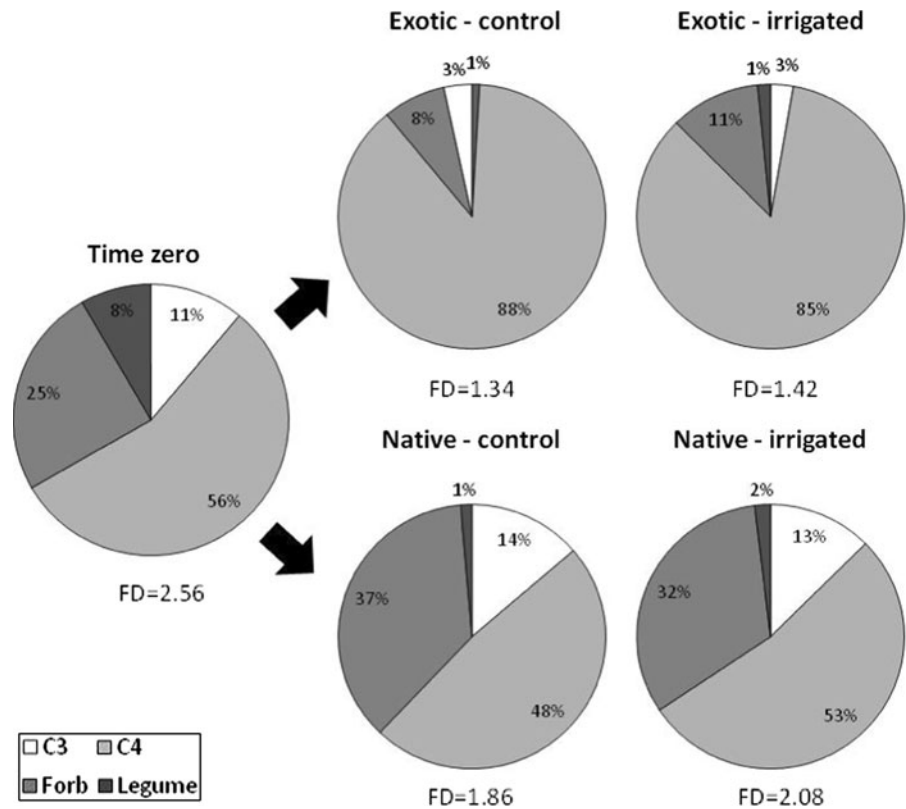
Functional group diversity was lower in exotic than native mixtures by the end of the first growing season (Fig. 1, $F_{1,7} = 11.1$, $P = 0.01$). Irrigation did not affect functional group diversity of either exotic or

native mixtures ($F_{1,7} = 2.9$, $P = 0.13$), nor did origin and irrigation interact ($F_{1,7} = 0.88$, $P = 0.38$). Exotic and native mixtures differed greatly in their relative abundance of functional groups (Fig. 1, MANOVA [Wilk's Lambda]: $F_{3,5} = 10.9$, $P = 0.01$). In exotic communities, C_4 grass abundance increased from 56 % at planting to 88 %, while in native communities C_4 grass abundance remained relatively unchanged (56–48 %). As a result, the final proportions of C_4 grasses differed significantly between natives and exotics ($F_{1,32} = 14.9$, $P < 0.001$). The abundances of C_3 grasses and forbs at harvest also differed between exotic and native mixtures (C_3 grasses $F_{1,32} = 21.9$, $P < 0.001$; forbs $F_{1,32} = 167.1$, $P < 0.001$). Exotic and native mixtures did not differ in the relative abundance of legumes ($F_{1,32} = 2.57$, $P = 0.12$). There was no significant effect of irrigation on relative abundances. The net result of these changes is that the C_3 : C_4 balance was much greater in native (roughly 50:50) than exotic communities (13:87) by the end of the first growing season.

Traits and changes in species relative abundance

A PCA of species traits found two principal components that together accounted for 68 % of the variance. The first had an eigenvalue of 2.75 and accounted for 39 %, and the second had an eigenvalue of 2.05 and accounted for 29 % of variance (Fig. 2). Loadings on the first principal component were dominated by size-related whole-plant traits, with the highest loadings by percent light capture (0.527), height (0.511), and biomass (0.478); all other loadings were $< |0.31|$. Change in relative abundance in mixture was correlated with the first component in both exotic ($r^2 = 0.25$, $P < 0.001$) and native communities ($r^2 = 0.22$, $P < 0.001$), but the functional group membership differed depending on origin. Species that had increases in relative abundance in exotic mixtures were all C_4 grasses, whereas, increasing native species included forbs, C_3 grasses and C_4 grass species (Fig. 2). Loadings on the second principal component were highest for leaf-level traits such as C:N ratio (-0.598), leaf N (0.494), SLA (0.483), and LA (0.397, all other loadings $< |0.18|$). Change in relative abundance in mixture was weakly correlated with the second component in native ($r^2 = 0.04$, $P = 0.05$) but not exotic ($P > 0.15$) communities.

Fig. 1 Relative abundances of exotic and native species in mixtures with and without irrigation. Means for functional group diversity of the different treatments are also provided



Leaf-level and whole-plant traits

Trait differences between native and exotic species depended on their functional group membership (Table 2). The exotic C₄ grasses, C₃ grasses and forbs had greater leaf area than their native counterparts (Fig. 3). SLA was significantly greater for exotic than native species of C₃ and C₄ grasses and legumes (Fig. 3b). Native C₃ grasses, forbs, and legumes had greater C:N ratios than their exotic counterparts (Fig. 3), but the C:N ratio of exotic (mean: 29.5, SE: 6.6) and native (mean: 29.48, SE: 2.09) C₄ grasses did not differ.

Height and whole-plant biomass also differed between natives and exotics depending on functional group membership. Exotic C₄ grasses were taller and had greater aboveground biomass than native C₄ grasses (Fig. 3). Conversely, native C₃ grasses were taller and had greater biomass (216.9 g) than exotic C₃ grasses (35.35 g). There was no difference in height or biomass between exotic and native forbs and legumes. The response of height and biomass to irrigation did not differ between exotic and native species for any

functional group (data not shown). Exotic C₄ grasses had greater peak light capture (68 %) than native C₄ grasses (51 %), while native C₃ grasses (55 %) had greater peak light capture than exotic C₃ grasses (19 %) in monoculture. Exotic and native forbs and legumes did not differ in peak light capture in monoculture.

Discussion

Novel communities composed of exclusively exotic species had less functional group diversity than native communities. The decline in functional group diversity was associated with plant traits. Interestingly, we found that the first-year decline in functional group diversity was associated with declines in species diversity and richness in the second growing season (Wilsey et al. 2011). The decline in functional group diversity in exotic communities was related to increases in dominance by C₄ grasses, primarily *Eragrostis curvula*, *Panicum coloratum*, or *Sorghum halepense*. Increases in relative abundance in mixture

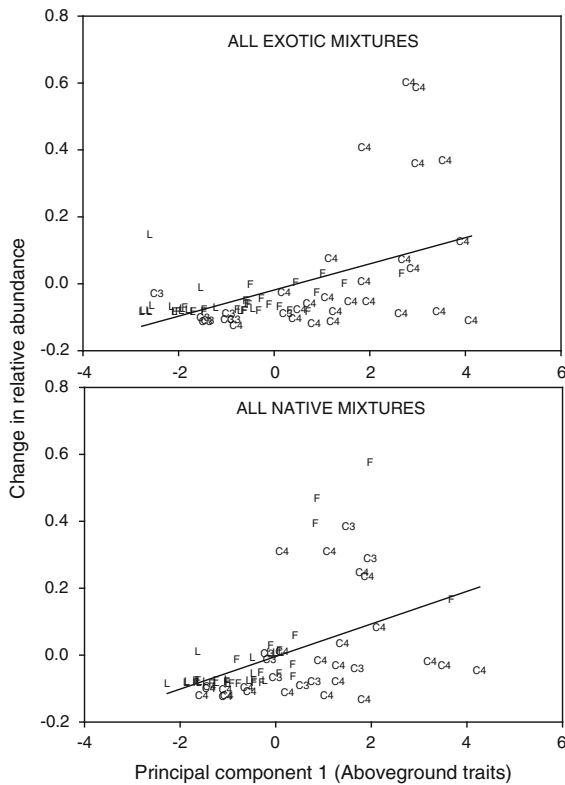


Fig. 2 Relationship between aboveground growth traits (principal component 1) and change in relative abundance by species in exotic (*top panel*) and native communities (*bottom panel*). Abbreviations denote functional group membership (C_4 = C_4 grass; C_3 = C_3 grass; F = C_3 Forb; L = C_3 Leguminous forb)

(i.e., yield) were correlated with high biomass, height, and light capture in monocultures for both native and exotic communities, but increasing exotic species were all C_4 grasses, whereas, increasing native species included forbs, C_3 grasses, and C_4 grass species. These community-level effects of exotic C_4 grasses were independent of leaf C:N ratio, consistent with our earlier findings (Wilsey and Polley 2006). This is consistent with results from subtropical parts of Australia, where problematic invasive species tended to be C_4 grasses that are tall with dense crowns and strong lateral spread (McIntyre et al. 2005). Species diversity of warm temperate grasslands is dependent on the success of C_3 species, especially forbs, which are often reduced by the dominance of C_4 grasses (Collins et al. 1998; Baer et al. 2003; Wilsey 2010). Our results suggest that C_4 dominance might be even greater when considering exotic species.

Table 2 Results from mixed model MANOVA (*df* and *F*) and ANOVA (*df* and *F*) for leaf area, specific leaf area (SLA), leaf C:N ratio, peak height, biomass, and light capture (PLC) among pairs, between origins (native vs. exotic), and origins and pairs

Effect	MANOVA		ANOVA												
	<i>df</i>	<i>P</i>	Leaf area		SLA		C:N		Height		Biomass		PLC		
			<i>df</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Block			1												
Pair (<i>P</i>)	102,583	<0.01	17,17	29.1	<0.01	10.0	<0.01	14.5	<0.01	12.4	<0.01	15.0	<0.01	11.0	<0.01
Origin (<i>O</i>)	6,101	<0.01	1,17	2.7	0.12	11.0	<0.01	4.9	0.04	0.6	0.47	0.6	0.45	0.1	0.37
<i>P</i> * <i>O</i>	102,583	<0.01	17,106	11.1	<0.01	6.3	<0.01	3.6	<0.01	6.1	<0.01	4.3	<0.01	4.4	<0.01
C_4					<0.01				0.98		0.01				0.01
C_3					<0.01				<0.01		<0.01				0.01
Forbs					0.01		0.09		<0.01	0.21			0.49		0.16
Legumes					0.80		<0.01		<0.01	0.05			0.38		0.24

P values are also given for a priori contrasts of origin with each functional group (C_4 grasses, C_3 grasses, Forbs, and Leguminous forbs)

^a Wilk's Lambda

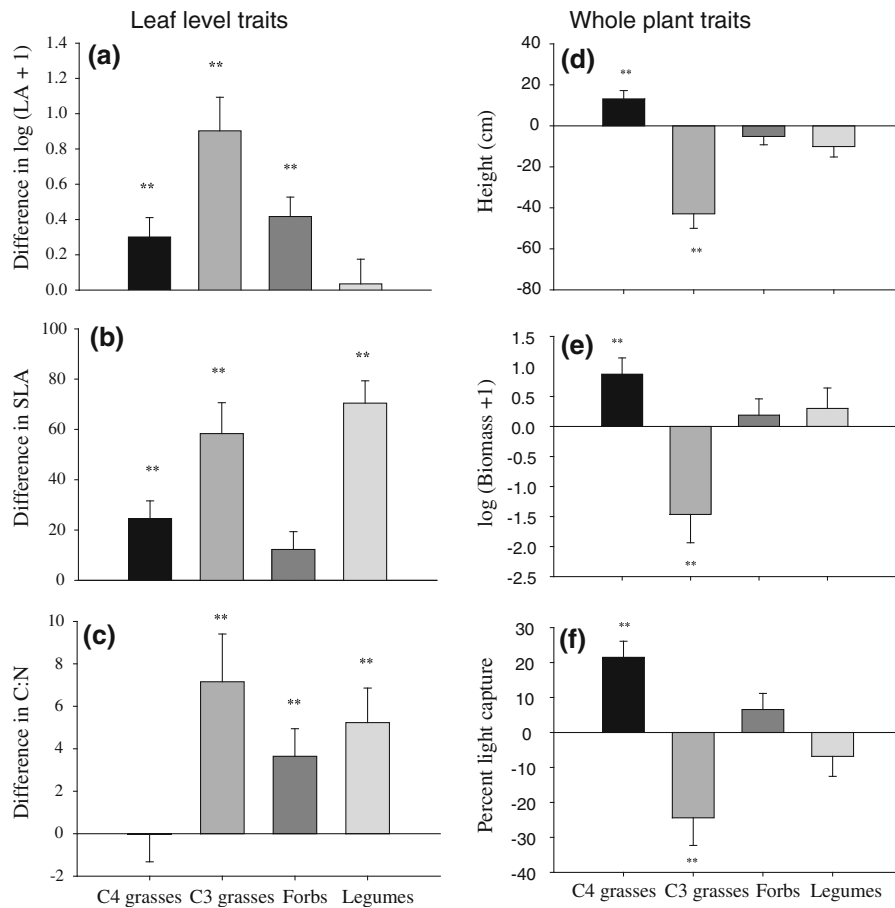


Fig. 3 a–c Differences in means between exotic and native species leaf traits **a** leaf area, **b** specific leaf area (SLA), **c** C:N ratios and whole-plant traits, **d** height, **e** biomass, **f** peak light capture by functional group. * $P < 0.05$, ** $P < 0.01$ (lsmeans

The traits that were correlated with differences among functional groups differed depending on origin. Both whole-plant and leaf-level traits explained C_4 grass success in exotic communities. A second contributing factor to functional diversity decline in exotic communities was the lower growth rate of exotic than native C_3 grass species. This effect is difficult to disentangle from C_4 dominance in our C_3 – C_4 mixtures. Competitive effects and responses often occur simultaneously (Goldberg and Landa 1991). Functional group diversity may have declined more in exotic than native communities because exotic C_4 grasses were more productive than natives, because exotic C_3 grass species were less productive than natives, or a combination of both. In native communities, C_3 species maintained their relative abundance. Native C_4 grasses were not as productive as their exotic pairs, which may

and SE, using six species of C_4 grasses, six species of C_3 forbs, origin, four species of C_3 legumes, and two species of C_3 grasses per origin, with $n = 4$ plots per species)

have resulted in less competitive stress on the other functional groups allowing them to maintain their relative abundance. The C:N ratio, which was consistently higher in native than exotic C_3 species, was the most consistent trait across species and functional groups in explaining C_3 plant success in native mixtures, perhaps a reflection of greater resource use efficiency, a slower potential rate of return on investments in leaves and longer leaf lifetimes (Wright et al. 2004). Several other studies have compared exotics to natives in their efficiency to utilize resources (Smith and Knapp 2001; Drenovsky et al. 2008; Feng and Fu 2008; Daneshgar and Jose 2009; Han et al. 2012). Funk and Vitousek (2007) suggested that greater photosynthetic nutrient use efficiency is a functional trait that enhances exotics competitive ability allowing them to invade nutrient poor systems in Hawaii.

We hypothesize that human selected traits led to increased dominance in exotic communities (Wilsey and Polley 2006; Wilsey et al. 2011), and this should be tested in the future by comparing introduced and source populations. Most of the exotic species that we used were intentionally introduced and most of the grasses were cultivars. The human selection involved in the introduction process may have resulted in increased aboveground competitive ability in exotic grass species (Lolicato and Rumball 1994), and this needs to be tested directly in future studies. In our experimental exotic communities, the species that grew tallest and were able to capture the most light (i.e., C₄ grasses) were able to increase in dominance. These fundamental differences between natives and exotics led to differences in functional group and eventually, species diversity.

In summary, this work demonstrated that resource-capture traits associated with exotic species are contributing to the lower diversity observed in exotic than native communities in the southern US (Wilsey et al. 2011). While our earlier work demonstrated drops in species diversity after 2 years (Wilsey et al. 2009, 2011), this new work concludes that novel ecosystems have less functional group diversity after the 1st year and that the simple plant traits that we measured were associated with the declines. Although further work is necessary in other systems, as well as with natives and exotics in mixed situations, our findings that functional group diversity remains higher in pure native than pure exotic communities (this study), and that spring green-up is earlier in exotic species and communities (Wilsey et al. 2011), implies that grasslands restored to native assemblages will function differently from those dominated by exotic species (Wilsey et al. 2009; Isbell and Wilsey 2011a, b; Mascaro et al. 2012).

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