

*Increasing native, but not exotic,  
biodiversity increases aboveground  
productivity in ungrazed and intensely  
grazed grasslands*

**Oecologia**

ISSN 0029-8549

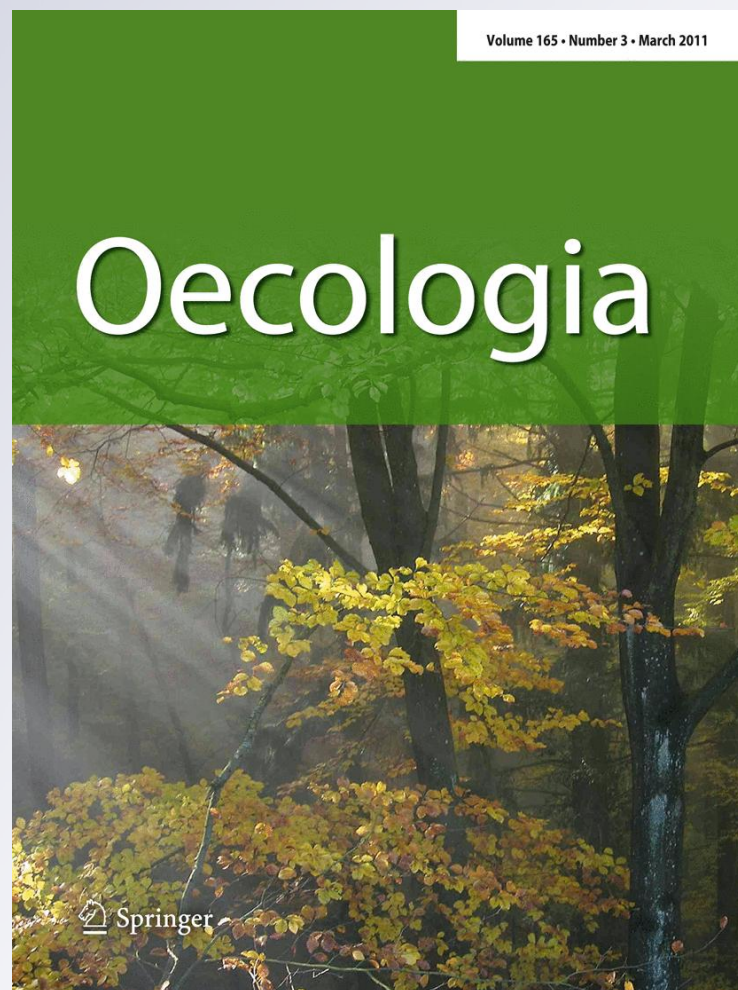
Volume 165

Number 3

Oecologia (2010) 165:771-781

DOI 10.1007/

s00442-010-1877-9



**Your article is protected by copyright and all rights are held exclusively by Springer-Verlag. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.**

# Increasing native, but not exotic, biodiversity increases aboveground productivity in ungrazed and intensely grazed grasslands

Forest I. Isbell · Brian J. Wilsey

Received: 28 May 2010 / Accepted: 30 November 2010 / Published online: 15 December 2010  
© Springer-Verlag 2010

**Abstract** Species-rich native grasslands are frequently converted to species-poor exotic grasslands or pastures; however, the consequences of these changes for ecosystem functioning remain unclear. Cattle grazing (ungrazed or intensely grazed once), plant species origin (native or exotic), and species richness (4-species mixture or monoculture) treatments were fully crossed and randomly assigned to plots of grassland plants. We tested whether (1) native and exotic plots exhibited different responses to grazing for six ecosystem functions (i.e., aboveground productivity, light interception, fine root biomass, tracer nitrogen uptake, biomass consumption, and aboveground biomass recovery), and (2) biodiversity–ecosystem functioning relationships depended on grazing or species origin. We found that native and exotic species exhibited different responses to grazing for three of the ecosystem functions we considered. Intense grazing decreased fine root biomass by 53% in exotic plots, but had no effect on fine root biomass in native plots. The proportion of standing biomass consumed by cattle was 16% less in exotic than in native grazed plots. Aboveground biomass recovery was 30% less in native than in exotic plots. Intense grazing decreased aboveground productivity by 25%, light interception by

14%, and tracer nitrogen uptake by 54%, and these effects were similar in native and exotic plots. Increasing species richness from one to four species increased aboveground productivity by 42%, and light interception by 44%, in both ungrazed and intensely grazed native plots. In contrast, increasing species richness did not influence biomass production or resource uptake in ungrazed or intensely grazed exotic plots. These results suggest that converting native grasslands to exotic grasslands or pastures changes ecosystem structure and processes, and the relationship between biodiversity and ecosystem functioning.

**Keywords** Land-use change · Novel ecosystems · Ecosystem functioning · Root biomass · Resilience

## Introduction

Species-rich native grasslands are frequently converted to species-poor exotic grasslands that are intensely grazed by livestock (Asner et al. 2004). The consequences of these changes for ecosystem functioning remain unclear because the effects of changing species richness, changing from native to exotic ecosystems, and increasing the intensity of grazing have often been considered separately, but may be non-additive. Ecosystem functioning includes all pools and fluxes of materials and energy in an ecosystem (Hooper et al. 2005). Previous studies have found that increasing biodiversity can increase biomass production and nutrient uptake in both terrestrial and aquatic ecosystems (reviewed by Hooper et al. 2005; Balvanera et al. 2006; Cardinale et al. 2006; Worm et al. 2006). Changing from native to exotic grasslands can increase aboveground productivity (Wilsey et al. 2009) and decrease root mass fraction (Wilsey and Polley 2006). Intense livestock grazing often

---

Communicated by Jason Kaye.

---

F. I. Isbell · B. J. Wilsey  
Department of Ecology, Evolution, and Organismal Biology,  
Iowa State University, Ames, IA 50011, USA  
e-mail: bwilsey@iastate.edu

F. I. Isbell (✉)  
Department of Biology, McGill University,  
1205 Avenue Docteur Penfield, Montreal,  
QC H3A 1B1, Canada  
e-mail: forest.isbell@mail.mcgill.ca

decreases aboveground productivity; and it can have negative, positive, or neutral effects on root biomass (reviewed by Milchunas and Lauenroth 1993; Asner et al. 2004). It has been hypothesized that intense grazing has different ecosystem effects in native and exotic grasslands (e.g., Kimball and Schiffman 2003), and that increasing species richness increases aboveground productivity similarly in ecosystems that are ungrazed or intensely grazed by livestock (Minns et al. 2001; Sanderson et al. 2004). However, the combined effects of these three changes remain unknown because no previous study has experimentally manipulated livestock grazing, plant species origin, and plant species richness.

The effects of intense grazing and changing from native to exotic-dominated ecosystems should be considered together because they often occur together, and could have non-additive effects. Exotic grassland species that were introduced by humans or favored by disturbance are often abundant when there is intense livestock grazing (D'Antonio and Vitousek 1992; Kimball and Schiffman 2003; Asner et al. 2004). Furthermore, many previous studies have found that intense livestock grazing can facilitate the spread of exotic species (e.g., Chaneton et al. 2002; Keeley et al. 2003; Kimball and Schiffman 2003; Best and Arcese 2009). These studies suggest that the spatial extent of exotic-dominated ecosystems, and the consequences of changing from native to exotic-dominated ecosystems, may partly depend on the presence and intensity of grazing. New experiments are needed to test for additive or non-additive effects of grazing and plant species origin.

Intense grazing may influence several ecosystem functions differently in native and exotic ecosystems because of trait differences between native and exotic species. Many plant species in grazing ecosystems exhibit strategies that allow them to compensate for biomass losses due to herbivory, such as shifting allocation of resources from belowground to aboveground tissues (McNaughton 1979; Wilsey et al. 1997). Exotic species that have experienced exceptionally intense grazing by exotic herbivores may better compensate for these biomass losses than native species that have evolved with less intense grazing by native herbivores (Simoes and Baruch 1991; Kimball and Schiffman 2003; Best and Arcese 2009). If exotic species recover aboveground biomass more quickly than native species, then intense grazing may reduce annual aboveground productivity and light interception more in native than in exotic ecosystems. Additionally, if exotic species recover aboveground biomass by shifting allocation of resources from roots to shoots, then intense grazing may reduce root biomass and nutrient uptake more in exotic than in native ecosystems. Native and exotic species may also be consumed at different rates by herbivores. Physical and chemical strategies for resisting grazing are common in

plants (Coley et al. 1985). Exotics may be consumed more than natives, if exotic species were selectively introduced as palatable forages. Alternatively, exotics may resist grazing and be consumed less than natives, if the shared history between exotic plants and herbivores has led to well-defended exotic plants. Thus, trait differences between native and exotic species may lead to differences in biomass production and resource uptake in native and exotic grazed ecosystems. If native and exotic ecosystems differ in important ways, then restoration and land management may benefit from further consideration of species origin.

New studies are also needed to determine whether biodiversity–ecosystem functioning relationships depend on grazing or species origin. There is considerable evidence that increasing species richness can increase biomass production and resource uptake in ecosystems that are not intensely grazed by livestock (reviewed by Hooper et al. 2005; Balvanera et al. 2006; Cardinale et al. 2006); and there is some evidence that increasing species richness can increase aboveground productivity in ungrazed managed ecosystems (Picasso et al. 2008; Weigelt et al. 2009). However, it remains unclear whether these results can be extrapolated to lands grazed by livestock (Sanderson et al. 2004) or in exotic ecosystems (Byrnes and Stachowicz 2009; Wilsey et al. 2009), both of which are becoming increasingly common worldwide (Asner et al. 2004; Hobbs et al. 2006; Wassenaar et al. 2007; Seastedt et al. 2008). Ecological studies in intensely grazed grasslands have considered trends in aboveground productivity, consumption (or, conversely, resistance to grazing), and recovery (resilience) after grazing across observed gradients of species diversity (McNaughton 1985, 1993a) rather than experimentally manipulating species diversity. Additionally, many agricultural studies in intensely grazed grasslands have been biased by non-randomly and non-systematically choosing plant species compositions (reviewed by Sanderson et al. 2004). For example, species that were expected to perform poorly at the study site have often been included in the high diversity plots, but not in the low diversity plots due to agronomic objectives (Sanderson et al. 2004). Thus, it remains unclear whether pasture productivity can be increased by increasing species richness, by introducing exotic species, or simply by identifying the most productive species (Minns et al. 2001; Sanderson et al. 2004; Schmid et al. 2008). Teasing apart these alternative hypotheses will require experiments that manipulate intense grazing, species richness, species origin, and species composition.

Several ecosystem functions are particularly relevant when considering the potential non-additive effects of intense livestock grazing, plant species origin, and plant species richness. Aboveground net primary productivity has been one of the most commonly considered ecosystem functions in grazing studies (reviewed by Milchunas and



Lauenroth 1993; Asner et al. 2004), native–exotic species comparisons (reviewed by Daehler 2003; Wilsey 2005), and biodiversity experiments (reviewed by Balvanera et al. 2006), in part because it integrates across numerous ecosystem functions at multiple trophic levels (McNaughton et al. 1989). Root biomass is also important because it is often a considerable fraction of the total biomass in grasslands (e.g., Reich et al. 2001; Wilsey and Polley 2006). Light interception and nitrogen uptake are particularly relevant because these resources can limit both diversity and productivity in subhumid and humid grasslands (Dybziński and Tilman 2007; Hautier et al. 2009). Rates of biomass consumption and recovery after grazing can be associated with plant diversity (McNaughton 1993a), and have been predicted to differ between native and exotic plant species (Kimball and Schiffman 2003).

The objectives of this study were to determine whether (1) intense grazing influences biomass production and resource uptake differently in native and exotic ecosystems, and (2) biodiversity–ecosystem functioning relationships depend on grazing or species origin. We conducted a factorial experiment that crossed grazing (ungrazed or intensely grazed once by cattle), plant species origin (native or exotic), and plant species richness (monoculture or 4-species mixture) treatments to test two hypotheses related to our first objective, and a third hypothesis related to our second objective. First, we tested whether intense grazing would decrease aboveground productivity and light interception more in native than in exotic plots, due to greater rates of aboveground biomass recovery by exotic species. Second, we tested whether intense grazing would decrease fine root biomass and tracer nitrogen uptake more in exotic than in native plots, also due to greater rates of aboveground biomass recovery by exotic species. Third, we tested whether increasing species richness increased biomass production (i.e., aboveground productivity and fine root biomass) and resource uptake (i.e., light interception and tracer nitrogen uptake) similarly in native and exotic plots that were either ungrazed or intensely grazed by cattle. Although numerous other hypotheses could have been considered, we focused on these novel hypotheses of non-additive effects because this was the first experiment to simultaneously manipulate livestock grazing, plant species origin, and plant species richness.

## Methods

### Study site

The BioGEN (biodiversity and grazing in exotic and native grasslands) field experiment was conducted at Iowa State University's Western Research and Demonstration Farm in

the loess hills region of Iowa, USA (42.06°N, 95.82°W). The study was established on a hill in an abandoned pasture, after the extant vegetation (dominated by *Bromus inermis*) was treated with glyphosate herbicide. The 30-year average annual temperature and precipitation are respectively 9.7°C and 782 mm. The mean annual temperature and precipitation were respectively 9.7°C and 561 mm during 2007, and 8.0°C and 835 mm during 2008. Soils are fine-silty, mixed (calcareous), mesic Typic Udorthents.

### Experimental design

Perennial native and exotic grassland plant species were carefully paired by phylogeny and functional group (Table 1). We included all exotic species that could be paired with a native species, that were known to be present in grasslands in the region, and for which propagules could be collected or purchased. Thus, our study was designed to test the effect of changing from native to exotic grasslands, rather than testing the effect of particularly invasive exotic species. Seedlings were grown in a greenhouse and transplanted into 1 × 1 m field plots on May 8–11, 2007. Seedlings that did not survive the first week were replaced. The planted density of 64 seedlings m<sup>-2</sup> was within the range observed in a nearby native prairie remnant (Losure et al. 2007). Weeds (i.e., non-planted species) were removed monthly during the growing season.

The experiment consisted of 128 (1 × 1 m) plots, which were separated by 1.1-m alleys, including 64 monocultures and 64 four-species mixtures. Mixtures had a full-factorial treatment structure for three factors: 2 grazing treatments (ungrazed or intensely grazed once by cattle) × 2 species origins (native or exotic) × 8 species compositions (combinations of species; Table 1) × 2 true replicates = 64 mixtures. Similarly, monocultures had a full-factorial treatment structure for three factors: 2 grazing × 2 origins × 8 species identities (i.e., a native–exotic pair; Table 1) × 2 true replicates = 64 monocultures. Mixture species compositions were systematically chosen (Table 1). Each four-species mixture included all four plant functional groups (Table 1), and the planted relative abundances of these functional groups were based on values observed in nearby native and exotic grasslands (C<sub>3</sub> grasses: 30 of 64 seedlings; C<sub>4</sub> grasses: 18 of 64; forbs: 14 of 64; legumes: 2 of 64) (Isbell 2010).

During the second year, 20 Angus steers (450 kg) consumed 74% of the standing crop biomass in one 24-h period, which was 40% of annual aboveground productivity, on June 10–11, 2008. The Iowa State University Institutional Animal Care and Use Committee approved all experimental protocols. Our intense grazing treatment was applied as a single, brief event to allow accurate

**Table 1** The native and exotic perennial grassland species used in this experiment were paired by functional and phylogenetic groups

Native species	Functional group	Phylogenetic group <sup>a</sup>	Compositions	Exotic species	Exotic species uses
<i>Andropogon gerardii</i> Vitman <sup>b</sup>	C <sub>4</sub> , G, N, R	Andropogoneae	<i>a, d, e, g</i>	<i>Miscanthus sacchariflorus</i> (Maxim.) Franch. <sup>b</sup>	Ornamental
<i>Sorghastrum nutans</i> (L.) Nash	C <sub>4</sub> , G, N, C	Andropogoneae	<i>b, c, f, h</i>	<i>Miscanthus sinensis</i> Andersson	Ornamental
<i>Pascopyrum smithii</i> (Rydb.) A. Löve	C <sub>3</sub> , G, N, R	Pooideae	<i>a, b, c, g</i>	<i>Bromus inermis</i> Leyss.	Forage
<i>Elymus canadensis</i> L.	C <sub>3</sub> , G, N, C	Triticeae	<i>d, e, f, h</i>	<i>Agropyron cristatum</i> (L.) Gaertn.	Forage
<i>Ratibida pinnata</i> (Vent.) Barnhart	C <sub>3</sub> , F, N, R	Asteraceae	<i>a, c, e, f</i>	<i>Leucanthemum vulgare</i> Lam.	Ornamental
<i>Brickellia eupatorioides</i> (L.) Shinnars	C <sub>3</sub> , F, N, T	Asteraceae	<i>b, d, g, h</i>	<i>Cichorium intybus</i> L.	Forage, Herb
<i>Astragalus canadensis</i> L.	C <sub>3</sub> , F, L, R	Fabaceae	<i>c, e, g, h</i>	<i>Coronilla varia</i> (L.) Lassen	Erosion, Forage
<i>Dalea purpurea</i> Vent.	C <sub>3</sub> , F, L, T	Fabaceae	<i>a, b, d, f</i>	<i>Trifolium repens</i> (L.)	Forage

For example, composition *a* native mixtures included *A. gerardii*, *P. smithii*, *R. pinnata*, and *D. purpurea*. Composition *a* exotic mixtures were also established, and included the four exotic species that were paired with these native species. Each species was present in four of the eight species compositions, and the frequency of pairwise species interactions in mixtures was also equal. Compositions *f* and *h* were randomly chosen for fine root biomass and tracer nitrogen uptake sampling

C caespitose, F forb, G grass, L legume, N nonleguminous, R rhizomatous, T taproot

<sup>a</sup> Forbs were paired by family, grasses were paired by subfamily or tribe

<sup>b</sup> Seedlings from this species pair were vegetatively propagated, all others were propagated from seed

quantification of biomass consumption. This treatment is comparable to some common grazing regimes (e.g., flash grazing, rotational grazing), but differs considerably from others (e.g., continuous grazing). The grazing treatment also included many aspects of grazing that clipping studies are unable to simulate, such as trampling. The intense grazing treatment was applied during mid-June because all of the plant species in our study were actively growing at this time. Unfortunately, one grazing enclosure was misplaced. Consequently, one of the two replicate “ungrazed” monocultures for *C. varia* was intensely grazed, and one of the two replicate “intensely grazed” composition *b* (Table 1) exotic mixtures was not grazed. Thus, rather than 16 plots per treatment combination, there were: NUO = 16, NGO = 16, NUF = 16, NGF = 16, EUO = 16, EGO = 17, EUF = 16, EGF = 15; where N = native, E = exotic, U = ungrazed, G = intensely grazed, O = one species, and F = four species.

#### Data collection

Several ecosystem functions were measured during year 2, including ecosystem processes (aboveground productivity, light interception, tracer nitrogen uptake, the proportion of aboveground biomass consumed by cattle, and the recovery of aboveground biomass after grazing) and a measure of ecosystem structure (fine root biomass). To quantify annual aboveground net primary productivity (ANPP), relative consumption, and recovery, vegetation was sampled with

both nondestructive (point-intercept) and destructive (clipping) methods. Peak biomass was harvested during year 2 (August 30, 2008) by clipping all biomass in all plots 3 cm above the soil surface, sorting by species, drying to constant mass, and weighing. Additionally, the vegetation in all plots was sampled with a nondestructive point-intercept method (Levy and Madden 1933) shortly before (June 3–4, 2008) and shortly after (June 12–13, 2008) the grazing event, and at peak biomass in year 2 (August 27–28, 2008). For point-intercept sampling, 40 pins were systematically dropped through the vegetation and the number of contacts for each plant species was recorded. A value of 0.5 was recorded for species that were present, but not in contact with any of the pins. By point-intercept sampling just before the clipping harvest, we were able to use regression to convert the point-intercept frequency data to biomass data ( $R^2$  for each species ranged from 0.72 to 0.97). This allowed us to quantify the amount of biomass consumed by cattle (consumed biomass = pre-grazing biomass – post-grazing biomass) and aboveground productivity (ANPP = peak biomass + consumed biomass).

We calculated relative measures of consumption and recovery. Consumption was quantified as the proportion of aboveground biomass that was consumed by cattle (consumption = consumed biomass/pre-grazing biomass). This measure of consumption was used because it controls for initial differences in standing biomass and thus is not confounded with annual aboveground productivity, as an

absolute measure of consumption would be. Recovery was quantified as the ratio of peak biomass in the intensely grazed (G) to the ungrazed (U) plots with the same species. That is,  $\text{recovery} = (\text{peak biomass})_G / (\text{peak biomass})_U$ . Thus, a recovery value of 1 indicated that the biomass of a particular plot had completely recovered to its ungrazed state (i.e., the species were resilient). Note that this measure of recovery is not confounded with annual above-ground productivity, although an absolute measure of recovery, such as the change in biomass after grazing, would be.

Light interception was quantified by measuring the photosynthetically active radiation (PAR) above and below the canopy. PAR was measured with a Decagon AccuPAR LP-80 light meter (Pullman, DC, USA) in all plots on August 27, 2008 before green tissues senesced. One measurement was taken above the canopy and two measurements were taken at ground level. Light interception was quantified as the percent of PAR that did not reach the ground level.

Fine root biomass was quantified from soil cores that were collected after the aboveground peak biomass harvest in year 2 (August 28, 2008). One soil core (5 cm diameter  $\times$  30 cm deep) was taken from the center of a subset of the mixtures ( $n = 16$ ) and monocultures ( $n = 48$ ) on August 30, 2008. Two of the eight mixture compositions were randomly chosen for belowground sampling (Table 1). The monocultures of all species in those two compositions were also sampled. Roots were hand-picked from each core, washed over a 250- $\mu\text{m}$  screen sieve, dried to constant mass, and weighed. Only two plots had coarse roots (i.e.,  $>1$  mm diameter), so fine root ( $<1$  mm diameter) biomass values are reported here.

A stable isotope tracer study was conducted to quantify tracer nitrogen uptake. Shortly after the grazing event (June 18, 2008), a labeled tracer was added to the same subset of plots where soil cores were later collected (Table 1). In each plot,  $\text{K}^{15}\text{NO}_3$  was added to the soil at a rate of  $0.1 \text{ g }^{15}\text{N m}^{-2}$ , homogeneously distributed to 36 points, which were arranged in a  $6 \times 6$  grid with 15 cm space between adjacent points. At each of the 36 points, 5 mL of  $0.037 \text{ mol K}^{15}\text{NO}_3/\text{L}$  was injected with a syringe to 1 cm depth. An equivalent amount of unlabeled  $\text{KNO}_3$  was added to the plots that were not included in the stable isotope tracer study.

Harvested shoot and root samples were analyzed for tracer nitrogen uptake. Shoot and root samples were sent to the Stable Isotope Mass Spectrometry Lab at Kansas State University, where they were dried, ground, weighed, packed, and analyzed with an isotope ratio mass spectrometer (Thermo Finnigan Delta Plus; Bremen, Germany) that was coupled to an elemental analyzer (CE 1110; Fisons Instruments, San Carlos, CA, USA). The shoot

sample for each species in each plot included all above-ground tissues for three randomly selected shoots for each species present. The root sample for each plot included all of the shallow (0–10 cm) roots from the core. The  $\delta^{15}\text{N}$  and % N were determined for each of these shoot and root samples.

The uptake of the  $^{15}\text{N}$  tracer ( $\text{g m}^{-2}$ ) was quantified as:

$$^{15}\text{N}_{\text{uptake}} = Y \times (\% \text{ N} / 100) \times (F_{\text{sample}} - F_{\text{std}}) \quad (1)$$

where  $Y$  is the biomass of the sample in the plot ( $\text{g m}^{-2}$ ), % N is the percent of the sample mass that was nitrogen,  $F_{\text{sample}}$  is the fractional abundance of  $^{15}\text{N}$  in the sample [i.e.,  $F = ^{15}\text{N} / (^{15}\text{N} + ^{14}\text{N})$ ], and  $F_{\text{std}}$  is the standard fractional abundance of  $^{15}\text{N}$  in atmospheric  $\text{N}_2$  ( $F_{\text{std}} = 0.00366$ ) (Buchmann et al. 1996). By adding the tracer, we created a signal that was strong enough to make several simplifying assumptions about isotope mixing and fractionation. Specifically, we assumed that (1) plant uptake of extant  $^{15}\text{N}$  was negligible compared to plant uptake of tracer  $^{15}\text{N}$ , (2) before enrichment, plants had the same fractional abundance of  $^{15}\text{N}$  as is observed in standard atmospheric  $\text{N}_2$  (i.e.,  $\delta^{15}\text{N} = 0$ ), and (3) fractionation was negligible (Fry 2006). These are reasonable assumptions for a tracer study such as this one because natural background  $\delta^{15}\text{N}$  values for plants typically range from only  $-8$  to  $+3\%$  (Peterson and Fry 1987), whereas the enriched plant sample  $\delta^{15}\text{N}$  values in our study ranged from 11.84 to 9,883.31‰. Thus, the tracer signal overwhelmed these other sources of variation. We report tracer nitrogen uptake as the percentage of added tracer nitrogen ( $0.1 \text{ }^{15}\text{N g m}^{-2}$ ) that was taken up by plants ( $^{15}\text{N}_{\text{uptake}}$ ).

#### Data analyses

We used general linear models in PROC GLM of SAS (SAS Institute, Cary, NC, USA) for all analyses. Above-ground productivity, light interception, fine root biomass, and tracer nitrogen uptake were analyzed with a full-factorial analysis of variance (ANOVA) model that included three fixed factors: planted richness (one or four species), grazing (none or intense), and origin (native or exotic). To determine how the effects of our grazing and origin treatments differed across species compositions in mixtures, these response variables were also analyzed with a full-factorial ANOVA model that included three fixed factors: grazing, origin, and species composition. To determine how the effects of our grazing and origin treatments differed across species identities in monocultures, these response variables were also analyzed with a full-factorial ANOVA model that included three fixed factors: grazing, origin, and species identity. Consumption and recovery measures in the intensely grazed plots were similarly analyzed, except that these ANOVA models did not

**Table 2** ANOVA results for the effects of the grazing (none or intense), species origin (native or exotic), and species richness (monocultures or four-species mixtures) treatments on aboveground productivity, light interception, fine root biomass, tracer nitrogen

uptake, consumption (i.e., the proportion of aboveground biomass consumed by cattle), and recovery (i.e., the ratio of peak biomass in intensely grazed plots to peak biomass in ungrazed plots with the same species)

Source	Aboveground productivity	Light interception	Fine root biomass	Tracer N uptake	Consumption	Recovery
Grazing (G)	$F_{1,123} = 3.22^\wedge$	$F_{1,123} = 4.05^*$	$F_{1,59} = 8.55^{**}$	$F_{1,60} = 8.91^{**}$		
Origin (O)	$F_{1,123} = 12.38^{***}$	$F_{1,123} = 1.49$	$F_{1,59} = 1.58$	$F_{1,60} = 0.00$	$F_{1,61} = 4.38^*$	$F_{1,61} = 6.21^*$
Richness (R)	$F_{1,123} = 9.83^{**}$	$F_{1,123} = 11.31^{**}$	$F_{1,59} = 1.77$	$F_{1,60} = 2.63$	$F_{1,61} = 0.00$	$F_{1,61} = 0.95$
G × O			$F_{1,59} = 7.02^*$			
G × R						
O × R	$F_{1,123} = 4.02^*$	$F_{1,123} = 2.80^\wedge$				
G × O × R						

Non-significant interactions ( $P > 0.15$ ) were pooled in the error term

$^\wedge P < 0.10$ ,  $* P < 0.05$ ,  $** P < 0.01$ ,  $*** P < 0.001$

include grazing as a factor. To meet assumptions of analyses, aboveground productivity and fine root biomass were natural logarithm transformed, and tracer nitrogen uptake and recovery were  $\ln(x + 1)$  transformed. Comparisons of treatment means were Tukey-adjusted to control for multiple comparisons. Non-significant interactions ( $P > 0.15$ ) were pooled into the error terms to determine the minimal adequate models.

## Results

### Aboveground productivity and light interception

Intense grazing decreased aboveground productivity by 25% (Table 2; Fig. 1a). Aboveground productivity was greater in native than in exotic plots, and greater in mixtures than in monocultures (Table 2; Fig. 1a). However, there was a significant origin × richness interaction (Table 2), indicating that increasing richness increased productivity by 42% in native plots, but increasing richness had no influence on productivity in exotic plots (Fig. 1a). Specifically, native mixtures (mean ± SEM:  $613.0 \pm 49.5 \text{ g m}^{-2} \text{ year}^{-1}$ ) were more productive ( $t = 3.64$ ,  $P = 0.002$ ) than native monocultures ( $432.6 \pm 49.5 \text{ g m}^{-2} \text{ year}^{-1}$ ), but exotic mixtures ( $248.5 \pm 49.5 \text{ g m}^{-2} \text{ year}^{-1}$ ) were not more productive ( $t = 0.80$ ,  $P = 0.855$ ) than exotic monocultures ( $253.5 \pm 49.5 \text{ g m}^{-2} \text{ year}^{-1}$ ) (Fig. 1a). Native mixtures were more productive than exotic mixtures for most, but not all, of the eight species compositions (origin × composition:  $F_{7,47} = 4.83$ ,  $P < 0.001$ ) (Fig. 2a). Native monocultures were more productive than exotic monocultures for some, but not most, of the eight species identities (origin × identity:  $F_{7,47} = 30.31$ ,  $P < 0.0001$ ) (Fig. 3a).

Intense grazing decreased light interception (Table 2; Fig. 1b). Specifically, more than 2 months after the grazing

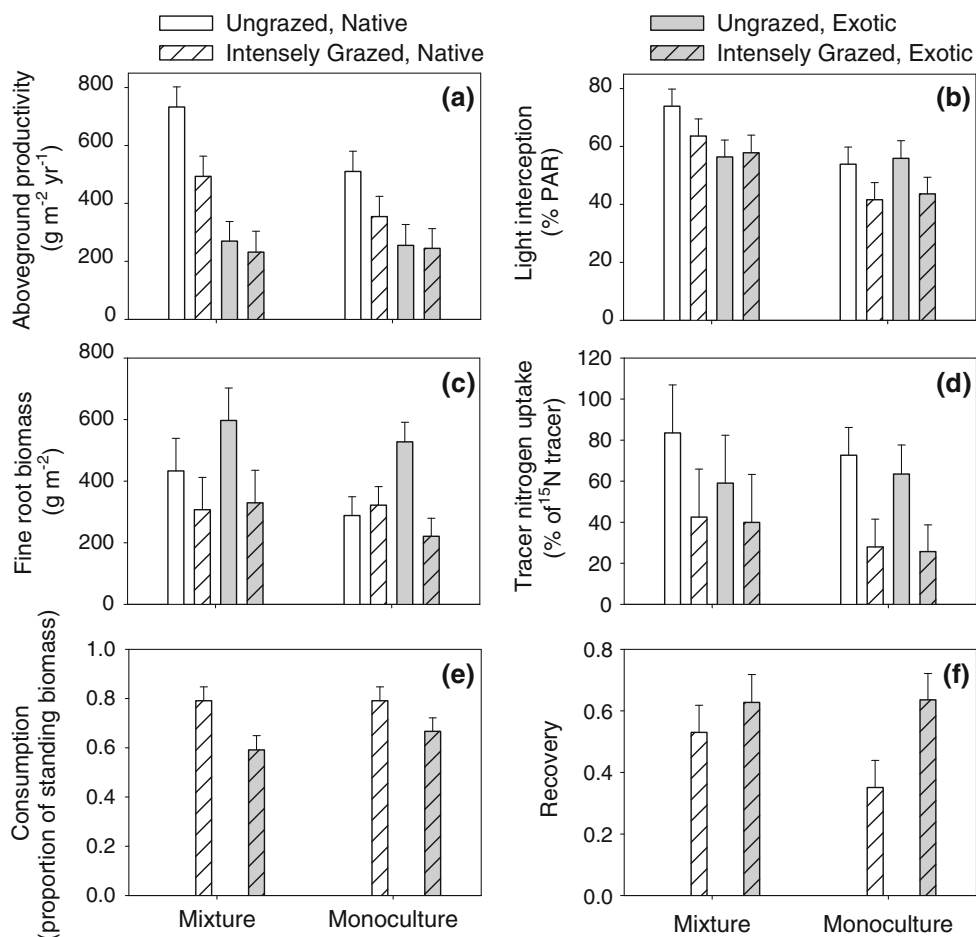
event, the proportion of PAR intercepted was 14% lower in the grazed ( $51.5 \pm 3.0\%$  PAR) than in the ungrazed ( $59.9 \pm 3.0\%$  PAR) plots. The proportion of PAR intercepted was greater in the mixtures than in the monocultures (Table 2; Fig. 1b). However, there was an origin × richness interaction (Table 2), indicating that increasing richness increased light interception by 44% in native plots, but increasing richness had no influence on light interception in exotic plots (Fig. 1b). Specifically, native mixtures ( $68.8 \pm 4.2\%$  PAR) intercepted more light ( $t = 3.56$ ,  $P = 0.003$ ) than native monocultures ( $47.8 \pm 4.2\%$  PAR), but exotic mixtures ( $56.7 \pm 4.2\%$  PAR) did not intercept more light ( $t = 1.20$ ,  $P = 0.631$ ) than exotic monocultures ( $49.6 \pm 4.2\%$  PAR) (Fig. 1b). Native mixtures intercepted more light than exotic mixtures for most, but not all, of the eight species compositions (origin × composition:  $F_{7,46} = 2.89$ ,  $P = 0.014$ ) (Fig. 2b). Native monocultures intercepted more light than exotic monocultures for some, but not most, of the eight species identities (origin × identity:  $F_{7,47} = 13.37$ ,  $P < 0.0001$ ) (Fig. 3b).

### Fine root biomass and tracer nitrogen uptake

Intense grazing influenced fine root biomass (Table 2; Fig. 1c). However, there was a significant grazing × origin interaction (Table 2), indicating that intense grazing decreased fine root biomass by 53% in exotic plots, but intense grazing did not influence fine root biomass in native plots (Fig. 1c). Specifically, fine root biomass was greater ( $t = 3.94$ ,  $P = 0.001$ ) in the ungrazed exotic ( $564.2 \pm 55.3 \text{ g m}^{-2}$ ) than in the intensely grazed exotic ( $267.1 \pm 52.7 \text{ g m}^{-2}$ ) plots, but was not significantly different ( $t = 0.19$ ,  $P = 0.997$ ) between the ungrazed native ( $344.1 \pm 53.9 \text{ g m}^{-2}$ ) and the intensely grazed native ( $337.5 \pm 53.9 \text{ g m}^{-2}$ ) plots. Fine root biomass did not depend on richness (Table 2; Fig. 1c). The grazing and



**Fig. 1** Aboveground productivity (a), light interception (b), fine root biomass (c), tracer nitrogen uptake (d), consumption (e), and the ratio of peak biomass in intensely grazed plots to peak biomass in ungrazed plots with the same species (f) in ungrazed or intensely grazed monocultures or four-species mixtures that were planted with either native or exotic species. PAR photosynthetically active radiation. Error bars 1 SEM



origin effects on fine root biomass did not depend on species composition in mixtures ( $P > 0.15$  for all composition interactions). Intense grazing decreased fine root biomass in monocultures more for some exotic species than for others (grazing  $\times$  origin  $\times$  species identity:  $F_{5,24} = 2.19$ ,  $P = 0.089$ ) (Fig. 3c).

Intense grazing decreased tracer nitrogen uptake by 54% (Table 2; Fig. 1d). Specifically, the proportion of the  $^{15}\text{N}$  tracer that was taken up by plants was 54% less in the intensely grazed ( $32.7 \pm 8.7\%$  uptake of tracer) than in the ungrazed ( $71.1 \pm 8.7\%$  uptake of tracer) plots. This grazing effect did not significantly differ across species composition in mixtures ( $P > 0.15$  for all grazing interactions), or species identity in monocultures ( $P > 0.15$  for all grazing interactions). Tracer nitrogen uptake did not depend on richness or origin (Table 2; Fig. 1d).

### Consumption and recovery

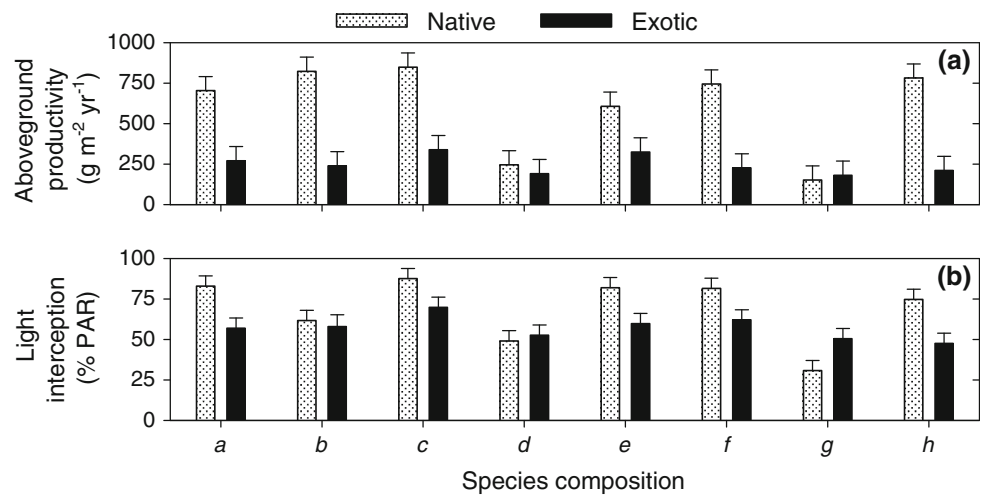
Consumption was decreased and recovery was increased in exotic compared to native grazed plots (Table 2; Fig. 1e, f). Specifically, the proportion of standing biomass consumed by cattle was 16% less in exotic ( $0.63 \pm 0.04$ ) than in

native ( $0.75 \pm 0.04$ ) grazed plots (Table 2; Fig. 1e). These differences in consumption did not depend on richness (Table 2; Fig. 1e) or species composition in mixtures (origin  $\times$  composition:  $P > 0.15$ ). There was an interaction between species origin and species identity in monocultures ( $F_{7,17} = 2.13$ ,  $P = 0.096$ ), indicating that native species were not consistently consumed more than exotic species for all species identities (Fig. 3d). Recovery was 30% less in native ( $0.44 \pm 0.06$ ) than in exotic ( $0.63 \pm 0.06$ ) grazed plots (Table 2; Fig. 1f). These differences in recovery did not depend on richness (Table 2; Fig. 1f), and did not significantly differ across species composition in mixtures (origin  $\times$  composition:  $P > 0.15$ ), or species identity in monocultures (origin  $\times$  identity:  $P > 0.15$ ). Consumption and recovery did not depend on richness (Table 2; Fig. 1f).

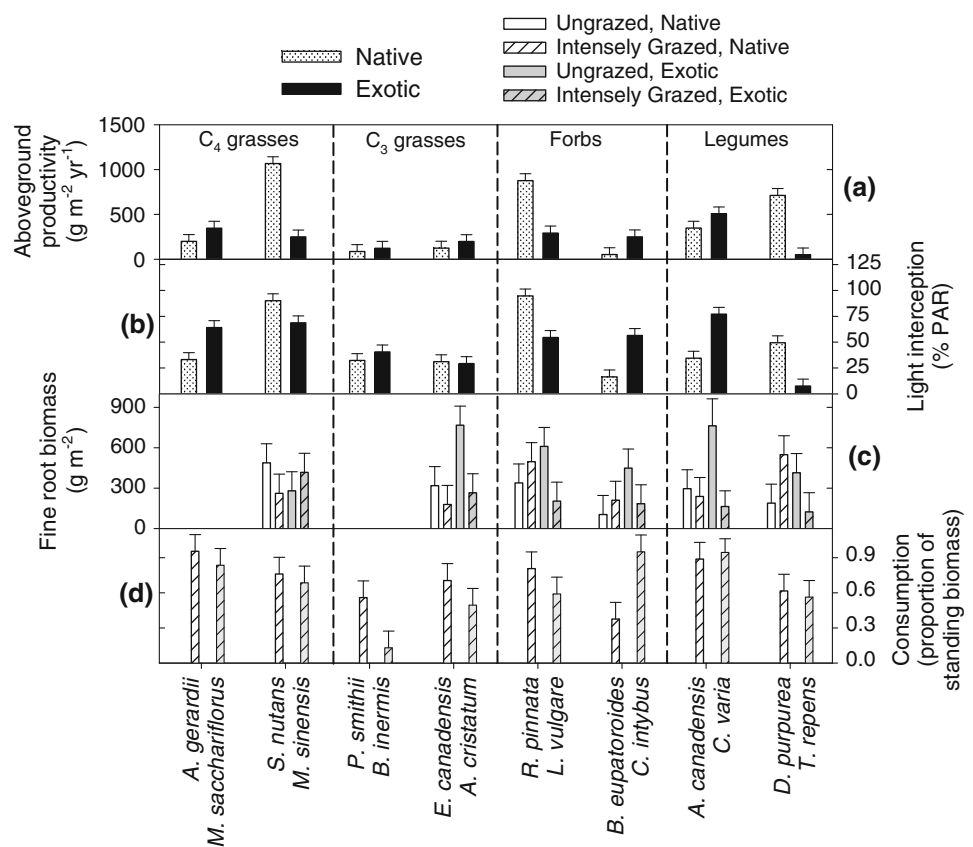
### Discussion

Our results suggest that native and exotic species respond differently to grazing, and that changing from native to exotic grazed grasslands can result in decreased rates of biomass consumption, and increased rates of aboveground

**Fig. 2** Effects of origin treatments depended on species composition in mixtures for aboveground productivity (a), and light interception (b). a–h Unique combinations of native or exotic species in 4-species mixtures. Table 1 indicates which species were included in each of these compositions. PAR Photosynthetically active radiation. Error bars 1 SEM



**Fig. 3** Effects of grazing or origin treatments depended on species identity in monocultures for: aboveground productivity (a), light interception (b), fine root biomass (c), and consumption (d). PAR Photosynthetically active radiation. Error bars 1 SEM



biomass recovery. Additionally, our results suggest that increasing the number of native species can increase aboveground productivity and light interception in both ungrazed and intensely grazed native ecosystems, but increasing the number of exotic species will not influence biomass production or resource uptake in ungrazed or intensely grazed exotic ecosystems. Here we further consider each of these main results.

Exotic species likely recovered consumed aboveground biomass by shifting allocation of resources from

belowground to aboveground tissues. Consistent with our second hypothesis, we found that exotic species more quickly recovered aboveground biomass following grazing than native species; and intense grazing decreased fine root biomass in exotic, but not in native, plots. Together these results suggest that exotic species recovered aboveground biomass more quickly than native species because they reallocated resources from belowground to aboveground tissues, while native species did not. Previous studies have found considerable variability in grassland plant responses

to grazing. Our results suggest that some of this variability may be explained by considering whether the plants in these studies were native or exotic. For example, grassland plants have exhibited a wide range of compensatory growth in previous studies, and this has led to some debate regarding whether grazing generally has positive or negative effects on plants (McNaughton 1993b; Painter and Belsky 1993). Furthermore, previous studies have found positive, negative, and neutral effects of grazing on root biomass (reviewed by Milchunas and Lauenroth 1993). The different responses to grazing exhibited by native and exotic species in our study suggest that, in addition to other factors known to interact with grazing (reviewed by Milchunas and Lauenroth 1993; Proulx and Mazumder 1998), plant species origin may be an important factor to consider when determining the effects of grazing on plants.

Interestingly, native species exhibited greater annual aboveground productivity than exotic species. Numerous previous studies have tested the hypotheses that exotic species are more productive or competitive than native species (reviewed by Daehler 2003; Vila and Weiner 2004; Wilsey 2005; Liao et al. 2008). However, it has been difficult to infer general differences between native and exotic species because many previous studies have compared exceptionally competitive exotic invasive species to relatively weak native competitors, or failed to consider numerous confounding environmental variables (reviewed by Daehler 2003; Vila and Weiner 2004; Wilsey 2005; Liao et al. 2008). Common garden grassland experiments that have carefully paired native and exotic species have found that exotic species can be more productive than native species (Wilsey and Polley 2006; Wilsey et al. 2009). However, comparative studies in intact grasslands have found that exotic species can be less productive than ecologically similar native species (Smith and Knapp 2001), and a review found that exotic species were not always more productive than native species (Daehler 2003). Together with the results reported here, these studies suggest that exotic species will not always be more productive than native species.

Our results suggest that increasing native species richness increases aboveground productivity and light interception in both ungrazed and intensely grazed ecosystems. We found that increasing species richness from one to four species increased aboveground productivity and light interception similarly in ungrazed and intensely grazed native plots, consistent with our third hypothesis. Increasing species richness can also increase aboveground productivity in mowed and fertilized grasslands (Weigelt et al. 2009) and in frequently harvested perennial forage mixtures (Picasso et al. 2008). Together, these findings suggest that results from previous studies in unmanaged ecosystems with no intense livestock grazing (reviewed by

Hooper et al. 2005; Balvanera et al. 2006; Cardinale et al. 2006) can be relevant for more intensely managed ecosystems (Minns et al. 2001; Sanderson et al. 2004).

Our results also suggest that changing the number of species in some exotic ecosystems will not influence biomass production or resource uptake. Interestingly, we found that increasing species richness from one to four species increased aboveground productivity and light interception in native, but not exotic, mixtures. Increasing species richness can increase productivity via positive complementarity effects, which result from niche partitioning or facilitation, positive selection effects, which favor highly productive species, or both (Loreau and Hector 2001). In our present study, we quantified complementarity and selection effects with Loreau and Hector's (2001) partition and found positive complementarity effects and negative selection effects in native mixtures, but no complementarity or selection effects in exotic mixtures (Isbell 2010). Thus, increasing native species richness increased aboveground productivity and light interception because there was niche partitioning or facilitation in native mixtures; but increasing exotic species richness did not increase biomass production or resource uptake because there was no niche partitioning, facilitation, nor selection effects in exotic mixtures. In a previous grassland biodiversity experiment, we found that increasing native species richness increased aboveground productivity, largely due to positive complementarity effects, and increasing exotic species richness increased aboveground productivity, largely due to positive selection effects (Wilsey et al. 2009). One previous marine biodiversity experiment compared the effects of increasing native versus exotic marine invertebrate species richness on water filtration, but found no significant effects of increasing native or exotic species richness (Byrnes and Stachowicz 2009). Many previous biodiversity experiments have included both native and exotic species in diversity treatments (e.g., Reich et al. 2001; Isbell et al. 2009). One way to test whether ecosystem functioning commonly depends more on native richness than on exotic richness would be to test whether the number of native species is a better predictor of ecosystem functioning than the total (i.e., native and exotic) number of species in previous biodiversity experiments.

Surprisingly, an exotic forage species that is common near our study site was one of the least productive species in our study. A long-standing question in ecology and agronomy is whether mixtures of species can outperform the single best species that they contain (McNaughton 1993a; Hector and Hooper 2002), and this question remains largely unresolved (Sanderson et al. 2004; Schmid et al. 2008). Many pastures and other exotic grasslands near our study site are almost exclusively dominated by an exotic  $C_3$  grass, *B. inermis*. For example, this single species composed

97.4% of the biomass in the abandoned pasture adjacent to our study site (Isbell 2010). Interestingly, this was one of the least productive and least consumed (i.e., most resistant) species in our study. This reveals that an important assumption of transgressive overyielding analyses, i.e., that the most productive species in monoculture are employed in agroecosystems, is false in at least some cases.

In conclusion, we found that native and exotic grazed ecosystems can differ in important ways. Intense grazing decreased fine root biomass in exotic, but not in native, plots. Exotic species were consumed less and recovered aboveground biomass more quickly than native species. Increasing the number of native species increased aboveground biomass production and light interception in both ungrazed and intensely grazed plots. However, increasing the number of exotic species did not influence any of the ecosystem functions that we measured. Further study with alternative grazing regimes and other plant species will help determine the generality of these results. These results suggest that converting native grasslands to exotic grasslands or pastures changes ecosystem structure and processes, and the relationship between biodiversity and ecosystem functioning.

**Acknowledgments** We thank Dan Isbell, Steve Goepferd, Leah Isbell, Kathryn Yurkonis, Joe Reynolds, Chris Johnson, Cedar Johnson, Kim Isbell, Joni Richmond, Robert Handler, Leanne Martin, Adam Heathcote, Wayne Roush, and Don Hummel for help with field work. This project was supported by a grant from the US National Science Foundation (DEB-0639417) to B.J.W. and a grant from the Leopold Center for Sustainable Agriculture to B.J.W. and F.I.I. We thank Jason Kaye and anonymous reviewers for helpful comments on an earlier version of this manuscript.

## References

- Asner GP, Elmore AJ, Olander LP, Martin RE, Harris AT (2004) Grazing systems, ecosystem responses, and global change. *Annu Rev Environ Resour* 29:261–299
- Balvanera P et al (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett* 9:1146–1156
- Best RJ, Arcese P (2009) Exotic herbivores directly facilitate the exotic grasses they graze: mechanisms for an unexpected positive feedback between invaders. *Oecologia* 159:139–150
- Buchmann N, Gebauer G, Schulze ED (1996) Partitioning of <sup>15</sup>N-labeled ammonium and nitrate among soil, litter, below- and above-ground biomass of trees and understorey in a 15-year-old *Picea abies* plantation. *Biogeochemistry* 33:1–23
- Byrnes J, Stachowicz JJ (2009) Short and long term consequences of increases in exotic species richness on water filtration by marine invertebrates. *Ecol Lett* 12:830–841
- Cardinale BJ et al (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989–992
- Chaneton EJ, Perelman SB, Omacini M, Leon RJC (2002) Grazing, environmental heterogeneity, and alien plant invasions in temperate Pampa grasslands. *Biol Invasions* 4:7–24
- Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. *Science* 230:895–899
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annu Rev Ecol Syst* 23:63–87
- Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annu Rev Ecol Evol Syst* 34:183–211
- Dybzinski R, Tilman D (2007) Resource use patterns predict long-term outcomes of plant competition for nutrients and light. *Am Nat* 170:305–318
- Fry B (2006) Stable isotope ecology. Springer, New York
- Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science* 324:636–638
- Hector A, Hooper R (2002) Darwin and the first ecological experiment. *Science* 295:639–640
- Hobbs RJ et al (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Glob Ecol Biogeogr* 15:1–7
- Hooper DU et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35
- Isbell FI (2010) Processes that influence biodiversity, ecosystem functioning, and stability in grasslands. PhD dissertation, Iowa State University, Ames
- Isbell FI, Polley HW, Wilsey BJ (2009) Species interaction mechanisms maintain grassland plant diversity. *Ecology* 90:1821–1830
- Keeley JE, Lubin D, Fotheringham CJ (2003) Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecol Appl* 13:1355–1374
- Kimball S, Schiffman PM (2003) Differing effects of cattle grazing on native and alien plants. *Conserv Biol* 17:1681–1693
- Levy EG, Madden EA (1933) The point method of pasture analysis. *N Z J Agric* 46:267–279
- Liao CZ et al (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol* 177:706–714
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76
- Losure DA, Wilsey BJ, Moloney KA (2007) Evenness-invasibility relationships differ between two extinction scenarios in tallgrass prairie. *Oikos* 116:87–98
- McNaughton SJ (1979) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am Nat* 113:691–703
- McNaughton SJ (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecol Monogr* 55:259–294
- McNaughton SJ (1993a) Biodiversity and ecosystem function of grazing ecosystems. In: Schulze ED, Mooney HA (eds) Biodiversity and ecosystem function. Springer, Berlin, pp 361–383
- McNaughton SJ (1993b) Grasses and grazers, science and management. *Ecol Appl* 3:17–20
- McNaughton SJ, Oesterheld M, Frank DA, Williams KJ (1989) Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341:142–144
- Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol Monogr* 63:327–366
- Minns A et al (2001) The functioning of European grassland ecosystems: potential benefits of biodiversity to agriculture. *Outlook Agric* 30:179–185
- Painter EL, Belsky AJ (1993) Application of herbivore optimization theory to rangelands of the western United States. *Ecol Appl* 3:2–9
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320



- Picasso VD, Brummer EC, Liebman M, Dixon PM, Wilsey BJ (2008) Crop species diversity affects productivity and weed suppression in perennial polycultures under two management strategies. *Crop Sci* 48:331–342
- Proulx M, Mazumder A (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79:2581–2592
- Reich PB et al (2001) Plant diversity enhances ecosystem responses to elevated CO<sub>2</sub> and nitrogen deposition. *Nature* 410:809–812
- Sanderson MA, Skinner RH, Barker DJ, Edwards GR, Tracy BF, Wedin DA (2004) Plant species diversity and management of temperate forage and grazing land ecosystems. *Crop Sci* 44:1132–1144
- Schmid B, Hector A, Saha P, Loreau M (2008) Biodiversity effects and transgressive overyielding. *J Plant Ecol* 1:95–102
- Seastedt TR, Hobbs RJ, Suding KN (2008) Management of novel ecosystems: are novel approaches required? *Front Ecol Environ* 6:547–553
- Simoës M, Baruch Z (1991) Responses to simulated herbivory and water-stress in two tropical C<sub>4</sub> grasses. *Oecologia* 88:173–180
- Smith MD, Knapp AK (2001) Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. *Int J Plant Sci* 162:785–792
- Vila M, Weiner J (2004) Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. *Oikos* 105:229–238
- Wassenaar T, Gerber P, Verburg PH, Rosales M, Ibrahim M, Steinfeld H (2007) Projecting land use changes in the Neotropics: the geography of pasture expansion into forest. *Glob Environ Change Hum Policy Dimens* 17:86–104
- Weigelt A, Weisser WW, Buchmann N, Scherer-Lorenzen M (2009) Biodiversity for multifunctional grasslands: equal productivity in high-diversity low-input and low-diversity high-input systems. *Biogeosciences* 6:1695–1706
- Wilsey BJ (2005) Importance of species replication in understanding plant invasions into North American grasslands. In: Inderjit S (ed) *Invasive plants: ecological and agricultural aspects*. Birkhauser, Switzerland
- Wilsey BJ, Polley HW (2006) Aboveground productivity and root-shoot allocation differ between native and introduced grass species. *Oecologia* 150:300–309
- Wilsey BJ, Coleman JS, McNaughton SJ (1997) Effects of elevated CO<sub>2</sub> and defoliation on grasses: a comparative ecosystem approach. *Ecol Appl* 7:844–853
- Wilsey BJ, Teaschner TB, Daneshgar PP, Isbell FI, Polley HW (2009) Biodiversity maintenance mechanisms differ between native and novel exotic-dominated communities. *Ecol Lett* 12:432–442
- Worm B et al (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–790