
Invasion by Non-Native Annual Grasses: The Importance of Species Biomass, Composition, and Time Among California Native Grasses of the Central Valley

Megan E. Lulow^{1,2,3}

Abstract

The Central Valley of California is noted for its dearth of remnant native grass populations and for low native grass seedling establishment within grasslands now dominated by non-native annual species. In contrast, remnant populations are common along the coast, and studies have shown an ability for seedlings and adults to compete with non-native annual grasses. The invasibility of well-established populations of native grasses in the Central Valley remains unclear. The objectives of this study were to compare the invasibility of native grasses differing in density and species composition and, given the species in this study, to assess the ability of mixes with greater species richness to resist invasion relative to their abilities in monoculture. In the Sacramento Valley of California, six species of native grasses were planted at three densities in monospecific and mixed-species plots. Percent cover of native perennial and non-native annual grasses was mea-

sured in years 2 and 3, and biomass was sampled in year 5. Native grass biomass and, to a lesser extent, species composition were important in explaining variation in non-native grass invasibility in the fifth year. Species-rich treatments did not experience less invasion than would be expected by the proportional invasibility of each species in monoculture. However, invasibility of plots consisting of slower growing, shorter statured species decreased over time, suggesting a successional benefit to diverse communities. This study demonstrates that established stands of native grasses in the Sacramento Valley can resist invasion by non-native annual grasses and that stand biomass is a particularly important factor in determining invasibility.

Key words: Central Valley, *Elymus glaucus*, *Elymus trachycaulus*, *Hordeum brachyantherum*, invasion, *Leymus triticoides*, *Melica californica*, *Nassella pulchra*, native grasses, overyielding, priority effects, species biomass.

Introduction

Invasion of California grasslands by non-native annual grasses from the Mediterranean region has resulted in one of the most rapid and extensive turnovers in plant community dominance known, with less than 2% of largely pristine grasslands remaining (Burcham 1957; Huenneke 1989; Mack 1989; Noss 1995). California native grasses primarily consist of perennial species; yet, the current cover of grasslands in California is heavily dominated by non-native annual species. There is interest in restoring areas with native grasses, as a goal in its own right, and for resource management purposes such as soil conservation and weed control (Bugg et al. 1991; Richards et al. 1998).

Both restoration attempts and ecological studies of native grasses have found that native perennial grass establishment from seed is greatly limited when growing within a background of non-native annual grasses (Jones & Love 1945; Bartolome & Gemmil 1981; Dyer et al. 1996; Stromberg & Kephart 1996; Dyer & Rice 1997, 1999; Brown & Rice 2000, but see Seabloom et al. 2003). The faster growth rate of non-native grasses shades native grass seedlings and limits seedling root development necessary to survive the intense summer drought season (Dyer & Rice 1999).

Restoration projects and experiments that have attempted to control non-native annual grasses during the establishment of native grass seedlings have shown that substantial native grass cover may be achieved within 2 years of seeding (Stromberg & Kephart 1996; Bugg et al. 1997). It is unclear to what extent productive, undisturbed stands of native grasses in the Central Valley are able to resist invasion, and whether they are able to create an environment suitable for their own recruitment.

Results from studies investigating the stability and invasibility of mature native grass stands are mixed, particularly results from studies conducted in the Central

¹ Department of Plant Sciences, University of California, Davis, CA 95616, U.S.A.

² Address correspondence to Megan E. Lulow, email mlulow@ucr.edu

³ Present address: Irvine Ranch Land Reserve Trust, 320 Commerce Drive Suite 150, Irvine, CA 92602, U.S.A.

Valley of California. Two studies indicate population stability of remnant native grass stands in a background of annual grasses (White 1967; Hamilton et al. 2002), whereas another found mortality rates to be 2–6% per year over a seven-year period (Dyer & Rice 1997). Studies that investigated newly established stands of native grasses (3–5 years old) found that they were able to limit annual grass productivity (Borman et al. 1991; Bugg et al. 1997; Brown & Bugg 2001; Seabloom et al. 2003; Corbin & D'Antonio 2004, but see Rein 1999); yet, among these studies, only two were conducted in California's Central Valley, and they had conflicting results. California's Central Valley experiences a particularly intense summer drought relative to the other study areas and contains proportionally fewer intact, remnant stands (Sampson et al. 1951; Heady et al. 1991; J. Clary 2003, University of California Davis, unpublished study). It is likely that the ability of native perennial grasses to compete with non-native annual grasses varies throughout the state of California due to regional climatic differences (Heady et al. 1991; Corbin & D'Antonio 2004).

On the scale of local plant community interactions, ecological theory and experimental studies suggest that, for a given invader, the invasibility of a community depends largely on the resident community composition, the species richness, or a combined effect of the two. The effect of increased species richness on ecosystem variables may be the result of (1) greater utilization of limiting resources through niche complementarity among species (for review, see Levine & D'Antonio 1999; Loreau & Hector 2001); or (2) a "sampling effect," where increases in species richness increase the likelihood that a dominant species occurs in the community (for review, see Levine & D'Antonio 1999; Wardle 2001). Intercropping experiments interested in testing whether increased yields in species-rich treatments were a result of niche complementarity compared species mixtures with their component species yields in monoculture. Obtaining yields greater than that expected based on the relative contribution of monoculture yields would result in "overyielding" (Trenbath 1974). The few invasion studies that have used replicate monocultures in a similar vein have been unable to explain patterns of invasion based on species richness alone (Crawley et al. 1999; Dukes 2002; Troumbis et al. 2002; Van Ruijven et al. 2003), or have found that invasibility increases with species richness (Palmer & Maurer 1997). Although two studies used multiple native grass species in their investigations of invasion by annual grasses in California grasslands (Bugg et al. 1997; Corbin & D'Antonio 2004), neither tested the effect of species richness on invasibility.

The likelihood of a species successfully invading a community may also depend on the existing community composition (Brown 1998). Results from an experiment on *Centaurea solstitialis* L. invasion into planted native grassland communities suggest that plants sharing similar resource-use patterns as the invader are less invulnerable than

those with dissimilar patterns (Dukes 2002). In addition, other studies have found that particularly robust species or functional groups, such as those with high levels of biomass, can greatly influence community invasibility (Borman et al. 1991; Symstad 2000). Native perennial grasses vary in their growth form characteristics and therefore likely vary in their resource utilization patterns; yet, there are no experimental studies that have investigated whether differences in invasibility among established California native grass species exist.

The purpose of this study was to compare mature stands of native grass species and species mixtures in their ability to resist invasion by non-native annual grasses. The questions posed were the following. (1) To what extent can non-native annual grasses invade mature stands of native grasses? (2) How important are the factors of native grass biomass and mix type (species composition) in influencing invasibility? (3) Based on the species in this study, do the mix types with multiple species overyield with respect to decreased invasibility?

Methods

Site Description

This study was conducted in the Sacramento Valley, at the Experimental Ecosystem (lat 38°31'N, long 121°48'W) administered by the University of California, Davis. The site was historically used for agricultural purposes; yet, it had been fallow for nearly 30 years prior to the initiation of the current experiment. The soil is classified as fine-silty, mixed, non-acid, thermic, Typic Xerorthent, with high natural fertility, moderate permeability, and a deep profile (Andrews 1990). The region is characterized as a Mediterranean climate, with particularly high summer temperatures for northern California. Mean precipitation at the study site is 484 mm/yr (1971–2000) and summer high temperatures average 32.6°C. Yearly (July–June) precipitation over the course of this study (1998–2003) was 324, 443, 368, 395, and 538 mm for July 1998–June 2003, respectively (National Oceanic Atmospheric Reference Climatological Station, University of California, Davis).

Prior to initiation of the study, plant cover was composed almost exclusively of Milk thistle (*Silybum marianum* (L.) Gaertner). As a result of site management (see below), the volunteer vegetation at the time of planting native grasses and throughout the remainder of the study was composed almost entirely of non-native annual grasses. Non-native annual grasses germinated from the existing seed bank the first year and continued to recruit seed each year, creating annual grass stands around all experimental plots throughout the study. Predominate non-native annual grasses included *Avena fatua* L., *Bromus diandrus* Roth, *Bromus hordeaceus* L., and *Hordeum murinum* L. *Lolium multiflorum* Lam. and *Vulpia myuros* C. Gmelin were a minor component of the non-native annual grass flora.

Experimental Design

The experiment was set up as five replicated blocks. Each block contained 10 distinct mixtures of native grasses, consisting of both monospecific and mixed-species plots (Table 1). Due to the large size of the study site (53×78 m), I chose a block design for randomization of treatment plots to account for the existence of any unforeseen environmental gradient, although no visual differences across the site were initially observed. In order to obtain a competitive gradient with annual grasses, I planted each of the 10 species mixtures at three planting densities: 4, 8, and 16 individuals/m². Thirty treatments (10 mixtures \times 3 densities) were randomly placed in 2×2 -m plots in each of the five replicate blocks (10 mixes \times 3 densities \times 5 replicates = 150 plots). Plots were spaced 3 m apart. I transplanted native grass species from four-month-old, cold-hardened, greenhouse-raised plugs ($3 \times 3 \times 7$ cm) in early March 1999 using templates for each of the three planting densities to guide placement of plugs. For equal spacing between individuals, I used a square planting pattern for the lowest density and a hexagonal pattern for the two higher densities. Plugs were inserted into holes made by a planting dibble. For mixed-species plots, equal proportions of plugs from each species were shuffled prior to planting within each plot. Any native grass transplants that died within the first year, primarily as a result of improper planting or herbivory from rabbits, were replaced with new transplants to maintain experimental densities.

Native grass species were selected that (1) were believed to have existed under similar environmental conditions as the study site; (2) covered a variety of native grass growth forms; and (3) were commercially available from a local grower. Species were paired to obtain two treatments contrasting in height and growth rate. Mixtures of three and six species were designed to contain more than one growth form within a treatment in order to test the idea that species in combination may resist invasion better than the expected invasibility based on the component species in monoculture.

Both species richness and functional diversity increase in the mixes with greater than two species; therefore, these

two types of diversity cannot be distinguished from each other in this study. Throughout the paper, I use the term species richness in a general sense (an increase in the number of species), not meaning to distinguish it from functional diversity. In addition, because there is only one replicate mix type at higher levels of species richness, conclusions about species richness with respect to overyielding should only be drawn for the native grass species in this study.

Management

This study was conducted in a restoration context, and some common management measures were implemented pre- and postplanting to control for non-native species. Site preparation consisted of discing the site during spring and following winter prior to planting and an application of the broad-spectrum herbicide Round-up (glyphosate) two weeks prior to planting the native grass transplants. In the late spring of the first growing season, the site was sprayed with the broadleaf herbicide Transline. Single applications of either Transline or 2-4D occurred in the early spring the following growing seasons, and a broadleaf herbicide was applied in the winter of the third year. Broadleaf herbicide was used for two reasons: (1) it simplified invasive plant competition to that of non-native annual grasses and (2) it replicated current restoration practice because it is common to apply broadleaf herbicide the first few years to assist in establishing native grasses in highly invaded grasslands in California. An additional technique commonly used in restoration practice is mowing just prior to the ripening of non-native annual grass seed in an attempt to reduce annual grass recruitment after planting native perennial grasses. I mowed the entire study site in the late spring of the second growing season (2000). Last, after initial fall rains and germination, I burned the site on 20 November of the fifth year to reduce thatch and increase light reaching the growth meristems of native perennial grasses. The burn was cool, removing loose thatch, but not killing the majority of non-native annual grass seedlings that had recently emerged.

The above management practices were implemented to increase the establishment of the native grasses and to simulate a realistic level of propagule pressure from

Table 1. Transplant plugs of the following species were planted into $2 \text{ m} \times 2\text{-m}$ plots of different mix types at three densities: 16, 32, and 64 plants/plot.

Species	Treatment Mix	Growth Type	Number of Species
<i>Elymus glaucus</i> (Blue wildrye)	EG	tall, fast	1
<i>Elymus trachycaulus</i> (Slender wheatgrass)	ET	tall, fast	1
<i>Leymus triticoides</i> (Creeping wildrye)	LT	tall, fast, rhizomes	1
<i>Melica californica</i> (California oniongrass)	MC	short, slow, weak rhizomes	1
<i>Nassella pulchra</i> (Purple needlegrass)	NP	short, slow	1
<i>Hordeum brachyantherum</i> (Meadow barley)	HB	short, fast	1
	NP/MC	short, slow	2
	LT/EG	tall, fast	2
	NP/EG/HB	combination	3
	All	combination	6

Nomenclature follows Hickman (1993).

non-native annual grasses relative to restoration projects in the region. The objective of the study was not to test establishment success of native grasses, rather it was to assess the ability of non-native annual grasses to invade mature stands of native perennial bunchgrasses.

Sampling

During the second, third, and fifth growing seasons (2000, 2001, and 2003), grasses were measured during April and May, encompassing the late flowering period of the grass species in this study. In the second and third growing season, percent cover of native and non-native grasses was estimated to the nearest percent using a 1×1 -m subplot divided into four quadrants. For these two years, the paired mix treatments and lowest density plots were not surveyed due to time constraints.

In the fifth year, biomass of native and non-native grasses was sampled within a 0.5×0.5 -m quadrat centered on one quadrant within each plot. Native grasses (by species), non-native grasses, and other vegetation were clipped separately, 2 cm from ground level, and placed into paper bags. Plant material was dried (57°C for 48 hr) and weighed. Because I was interested in how non-native grasses responded to a range of native grass biomass from each mix type, quarters of plots with the greatest survival of planted native species were chosen because they best reflected the original range of planted densities.

The area surrounding each plot received the same management as the experimental plots (other than native transplants) and produced prolific non-native annual grass cover. The abundance of non-native annual grasses around the plots suggested a large seed reserve on the site and sufficient source of seed rain for the plots.

Statistics

The focus of analyses is on the fifth growing season (2003). To inform results in 2003, some data are also presented from earlier years. I considered planted native grasses the independent variable, because their density was manipulated across treatments, and non-native grasses the dependent variable. For analyses, I did not label the different density plots categorically for each mix type because their purpose was to create a gradient in native grass biomass from which to assess non-native grass invasibility.

I conducted a correlation analysis to assess the influence of variation in native grass biomass (created from the three planting densities) on variation in non-native grass biomass, averaged across the five replicate blocks, for all mix types (SAS Institute 2002). In order to distinguish between the effects of native grass biomass versus mix type on non-native grass biomass, I ran an analysis of covariance (ANCOVA) with non-native grass biomass as the dependent variable, native grass biomass as the covariate, and mix type as the independent variable. I put the following factors in the model statement: block, native

grass biomass, mix, and native grass biomass \times mix. When the interaction was not significant, another ANCOVA was run excluding the interaction term. This was followed by a Tukey–Kramer Honestly significant difference (HSD) analysis to compare mix types ($p < 0.05$). This test also provided information on the per-unit biomass effect of native grass mixes on non-native grass biomass production.

For general comparisons of native and non-native grass biomass among mix types (without controlling for the effect of native grass biomass), two analyses of variance (ANOVAs) were run with mix type as the independent variable and either native or non-native grass biomass as the dependent variable. These tests were run on the average of the three density treatments for each mix type. Tukey–Kramer HSD analyses were used for multiple comparisons ($p < 0.05$). Both native and non-native grass biomass values were square root transformed to obtain homogeneity of variances. This same procedure was followed for the 2000 and 2001 datasets, with the following exceptions: fewer treatments were sampled (see Experimental Design), analyses are only reported for non-native grasses as a function of mix type, percent cover was used as a measure of abundance instead of biomass, and density measurements were treated categorically and included as an additional term in the ANOVA. With no interaction between mix type and density, the multiple comparison tests were run on the average of the densities. Data were arcsine square root transformed both years.

The invasibility of a community may represent the sum of the abilities of each species in monoculture to resist invasion, or it may overyield by falling short of this sum as a result of interactive effects among species (i.e., higher order effects). To test whether overyielding as applied to community invasibility existed in treatments with greater species richness, the proportion of cover (or biomass) for each native species in a given polyculture treatment was multiplied by the amount of non-native grass cover (or biomass) in each native species' monoculture treatment. The sum of these amounts among species in a given polyculture would then represent "expected" invasibility, representing additive species effects, based on species respective monocultures. If the actual amount of non-native grass in this polyculture treatment were lower than this expected amount, it would suggest that combining species would lead to lower invasibility, thereby overyielding through some higher order effect that would not be achieved by each species existing alone.

Results

Native Grass Biomass and Species Composition

Overall, there was a strong negative correlation between native grass biomass and non-native grass biomass across mixes (Fig. 1; $r = -0.87$). Across all plots, native grass biomass ranged widely from 0 to 2,398 g/m and had a

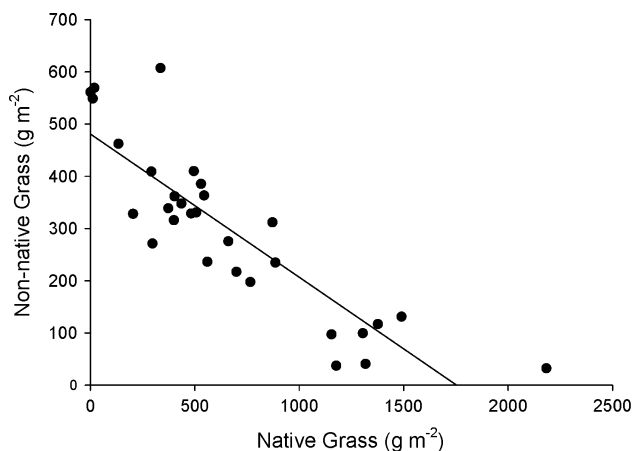


Figure 1. Regression of mean non-native and native grass biomass across all mix types. Correlation coefficient $r = -0.87$.

maximum yield nearly three times that of non-native annual grasses at 805 g/m.

Overall, there was a significant interaction between the effects of mix type and native grass biomass and no significant block effect (Table 2). This suggests that depending on the mix type, the relationship between native grass biomass and non-native grass biomass varies.

Two mix types appear to be responsible for this interaction: *Leymus triticoides* and *L. triticoides/Elymus glaucus*. When these mixes are excluded from the ANCOVA, mix type and native grass biomass are significant effects, but there is no longer an interaction (Table 2). Looking at the distribution of plot points for each mix type (Fig. 2), it also appears that this interaction is the result of mixes including *L. triticoides*. *Leymus triticoides* and *L. triticoides/E. glaucus* are the only mix types lacking a negative relationship between native and non-native grass biomass, with their points distributed horizontally across the native grass axis (Fig. 2). Unlike the other mix types and species, lower levels of *L. triticoides* biomass were able to exclude non-

native grass biomass similarly to higher levels of its biomass. Furthermore, the lower end of the range of native grass biomass values for *L. triticoides* and *L. triticoides/E. glaucus* corresponds to the upper end of the range of native biomass values for the other mix types (Fig. 2). These results may be explained by the growth habits and robustness of *L. triticoides*; it is fast growing and tall, and the only native grass that produces robust rhizomes.

Controlling for the effect of native grass biomass by including it as a covariate, the effect of mix type on non-native grass biomass can be compared among the mix types (Table 3). Three species accounted for significant differences among the mix types: *Melica californica* was the most resistant to non-native grass invasion, and *Hordeum brachyantherum* and *Elymus trachycaulus* were the least resistant (Table 3).

Species and biomass levels may be inherently confounded because larger species have a tendency to produce greater biomass, despite individual variation. It is therefore useful to compare the abilities of different mix types to resist invasion on a general level, without controlling for the influence of biomass per se, as was done in the ANCOVA above. ANOVA including only mix type as the independent variable in the model revealed significant variation in non-native and native grass biomass among mix types (Table 2; Fig. 3).

By 2003, the native grass *H. brachyantherum* had suffered such high mortality that its mean biomass was 97–99% less than the native biomass in any other treatment, with an average biomass of only 11g/m (Fig. 3). Therefore, I used the *H. brachyantherum* plots to serve as a control, representing levels of non-native grass biomass without interference from native grass biomass. With the exception of *E. trachycaulus*, all mix types significantly reduced non-native grass biomass relative to this control treatment (Fig. 3). In seven of the eight remaining mixes, biomass of non-native grasses was >43% lower, and in *L. triticoides*, it was >90% lower than the control.

Table 2. ANOVA (2003) testing the effects of (1) native grass biomass (covariate) and mix type on non-native grass biomass and (2) mix type (no covariate) on non-native and native grass biomass.

	ANCOVA (All Mixes)	ANCOVA ^a (No LT, LT/EG)	ANCOVA ^b (No LT, LT/EG)	ANOVA	ANOVA
Dependent variable	NNG biomass	NNG biomass	NNG biomass	NNG biomass	NG biomass
Whole model	$F_{[20,126]} = 13.11$; $p < 0.0001$	$F_{[16,100]} = 6.75$; $p < 0.0001$	$F_{[9,107]} = 12.12$; $p < 0.0001$	$F_{[9,40]} = 20.79$; $p < 0.0001$	$F_{[9,40]} = 48.2$; $p < 0.0001$
NG biomass	$F_{[1,126]} = 5.50$; $p < 0.02$	$F_{[1,100]} = 4.86$; $p < 0.03$	$F_{[1,107]} = 27.4$; $p < 0.0001$	—	—
Mix type	$F_{[9,126]} = 2.54$; $p < 0.01$	n.s.	$F_{[9,107]} = 2.87$; $p < 0.009$	$F_{[9,40]} = 20.79$; $p < 0.0001$	$F_{[9,40]} = 48.2$; $p < 0.0001$
NG biomass × mix type	$F_{[9,126]} = 2.19$; $p < 0.03$	n.s.	—	—	—
Block	$F_{[1,126]} = 4.83$; $p < 0.03$	n.s.	n.s.	n.s.	n.s.

NNG = non-native grass; NG = native grass; LT = *Leymus triticoides*; EG = *Elymus glaucus*.

^a Including interaction term.

^b Interaction term excluded because insignificant in test a.

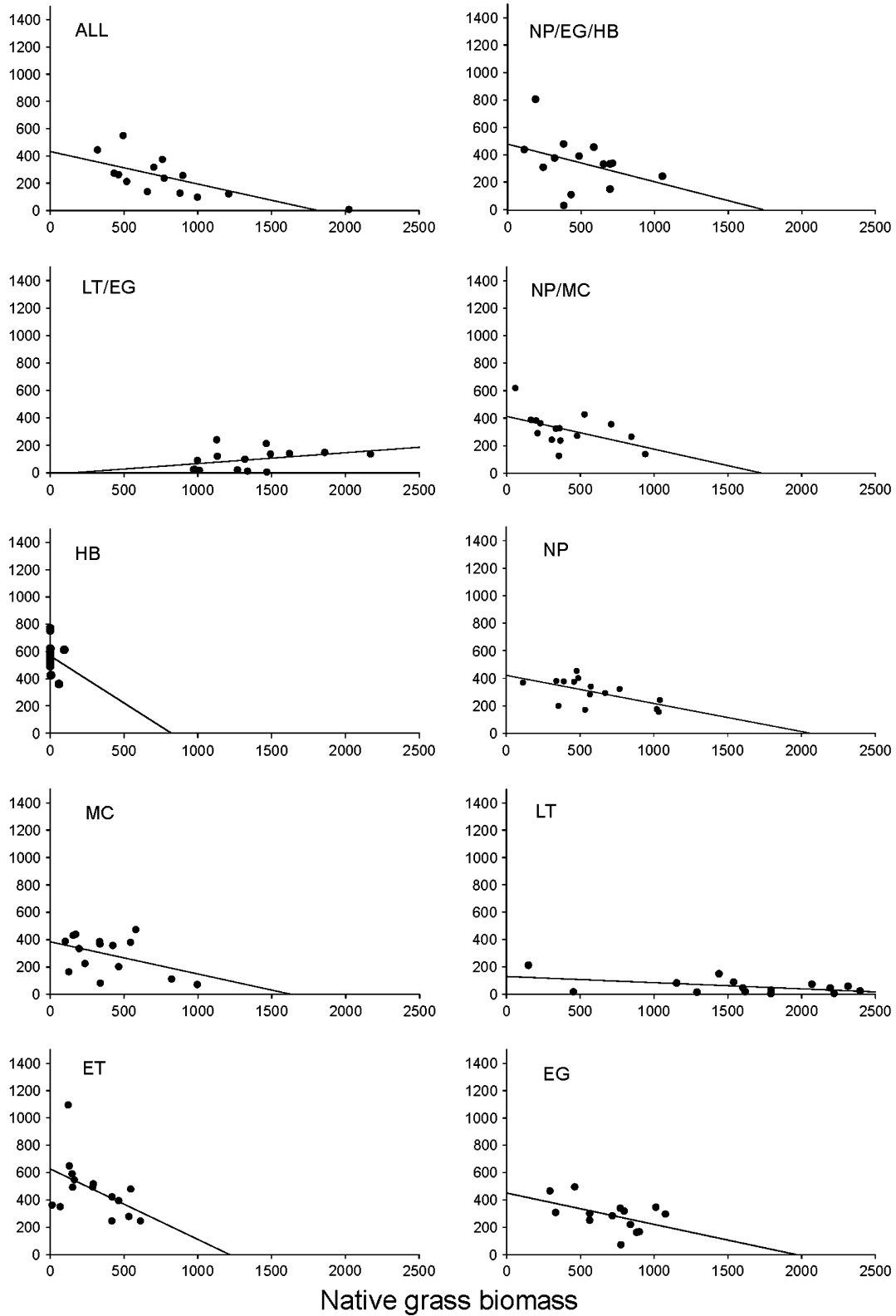


Figure 2. Regression of non-native and native grass biomass across all plots for each mix type. EG = *Elymus glaucus*; ET = *Elymus trachycaulus*; HB = *Hordeum brachyantherum*; LT = *Leymus triticoides*; MC = *Melica californica*; NP = *Nassella pulchra*.

Table 3. Variation in non-native grass biomass among mix types (main factor), while controlling for variation in native grass biomass (covariate).

Mix Type	Least Squares Mean of NNG Biomass (m ²)	Standard Error	Significance
HB	451	39	A
ET	437	34	A
EG	349	36	AB
NP/EG/HB	349	34	AB
NP	334	33	AB
All	329	37	AB
NP/MC	304	32	AB
MC	277	32	B

Treatments not sharing a letter are significantly different ($p < 0.05$, Tukey–Kramer HSD). EG = *Elymus glaucus*; ET = *Elymus trachycaulus*; HB = *Hordeum brachyantherum*; MC = *Melica californica*; NP = *Nassella pulchra*; NNG = non-native grass.

Comparisons of native and non-native grass biomass across treatments show that only *H. brachyantherum* and *E. trachycaulus* had less native than non-native grass biomass. In contrast, native grass biomass of *Nassella pulchra*, *E. glaucus*, and *L. triticoides* obtained up to three times the highest non-native biomass value (Fig. 3).

General results from 2000 and 2001 are consistent with those from 2003; the percent cover of non-native grasses varied among mix types, declined with higher native grass planting densities, and showed no interaction between mix type and planting density (2000: mix type, $F_{[7,30]} = 16.2$ $p < 0.0001$; density, $F_{[1,30]} = 28.7$ $p < 0.0001$; 2001: mix type, $F_{[7,62]} = 29.2$ $p < 0.0001$; density, $F_{[1,62]} = 35.8$ $p < 0.0001$). The native species used in this study vary in

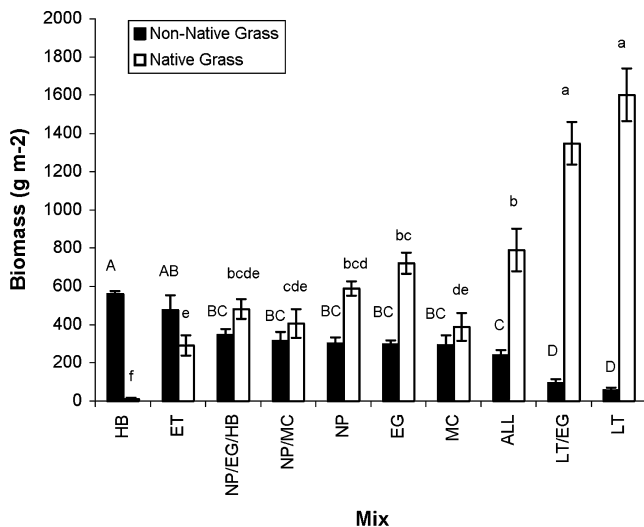


Figure 3. Mean biomass of each native and non-native grass within each mix type in 2003. Treatments differing in native grass density were averaged for each mix type. Treatments not sharing a letter are significantly different ($p < 0.05$, Tukey–Kramer HSD); non-native grass = uppercase, native grass = lowercase. EG = *Elymus glaucus*; ET = *Elymus trachycaulus*; HB = *Hordeum brachyantherum*; LT = *Leymus triticoides*; MC = *Melica californica*; NP = *Nassella pulchra*.

growth rate, height, and presence of rhizomes, and some informative trends are apparent. In the second growing season (2000), the single-species plots with the fastest growing, tallest species (*E. glaucus*, *E. trachycaulus*, and *L. triticoides*) ranked the lowest in non-native grass cover ($F_{[7,23]} = 17.5$ $p < 0.0001$). The following year, a slower growing species, *N. pulchra*, ranked lower in non-native grass cover than two of these species ($F_{[7,39]} = 21.0$ $p < 0.0001$) (Table 4). By the fifth growing season (2003), the other slow-growing species (*M. californica*) ranked lower than these species, and *E. trachycaulus* ranked second in the greatest amount of non-native grass growth (Tables 2 & 4). Although some of these differences are not significant in a given year, there appears to be a general trend among species and years.

Leymus triticoides, the only native species that grows prolific, long, and stout rhizomes, had the greatest above-ground biomass and the lowest invasibility throughout the study period (with the exception of its paired mix with *E. glaucus*, for which it accounted for on average greater than 80% of the mix by 2003; Table 5). *Melica californica* forms corms and short rhizomes, and this species stands out by resisting invasion as well as other species that had greater aboveground biomass (Table 3; Fig. 3).

Species Richness and Overyielding

None of the four polycultures (ALL, *N. pulchra*/*E. glaucus*/*H. brachyantherum*, *L. triticoides*/*E. glaucus*, and *N. pulchra*/*M. californica*) were less invasible than their most suppressive species in monoculture (Fig. 2). Table 5 compares the amount of non-native grass that invaded each treatment to the amount that would be expected had the native species within each polyculture responded additively to invasion. In both polycultures sampled in 2000, and in all the polycultures sampled in 2003, this expected number tended to track, or be slightly less, compared with the actual amount of non-native grass. This suggests native species acted additively, or slightly increased, in their cumulative invasibility by existing in polyculture. The relative abundance of native species in polyculture changed from 2000 to 2003, declining in species evenness (Table 5). Despite this decline in species evenness, the results described above were consistent between years.

Discussion

Native Grass Biomass

Based on the average native grass biomass, almost all the mix types obtained greater biomass than the non-native grasses, and non-native grass biomass was 44–90% lower in most mixes than in the control plot in the fifth growing season. In addition, total native grass biomass was strongly negatively correlated with non-native grass biomass, suggesting that native grasses interfere with the growth of non-native annual grasses. These results support studies

Table 4. Relative ranking of non-native grass abundance (m²) across years. Mixes LT/EG and NP/MC are not shown because they were not sampled in 2000 and 2001.

Ranking 2000	Percent Cover (SE)	Ranking 2001	Percent Cover (SE)	Ranking 2003	Biomass (SE)
MC	62(7) a	HB	77(3) a	HB	560(27) a
NP/EG/HB	33(7) b	MC	73(4) ab	ET	477(54) ab
NP	26(5) bc	ALL	51(4) bc	NP/EG/HB	341(50) bc
HB	25(4) bc	NP/EG/HB	51(4) bc	NP	301(24) bc
All	23(6) bc	EG	45(7) c	EG	298(30) bc
EG	16(3) bcd	ET	45(4) c	MC	293(36) bc
ET	13(4) c	NP	29(5) cd	ALL	243(39) c
LT	7(3) d	LT	11(4) d	LT	58(15) d

Treatments not sharing a letter are significantly different ($p < 0.05$, Tukey-Kramer HSD). EG = *Elymus glaucus*; ET = *Elymus trachycaulus*; HB = *Hordeum brachyantherum*; LT = *Leymus triticoides*; MC = *Melica californica*; NP = *Nassella pulchra*.

that investigated the ability of planted native grass stands to compete with invading non-native grasses in coastal northern California (Corbin & D'Antonio 2004) and in the southern Coast Range (Seabloom et al. 2003). In addition, the initial densities of native grasses in my study were low (Brown & Bugg 2001; Corbin & D'Antonio 2004), and biomass of established native and non-native grasses was substantially greater compared with other studies (Seabloom et al. 2003; Corbin & D'Antonio 2004). These

results are somewhat surprising given the intense summer drought in the Central Valley and few remnant native grass stands relative to coastal regions of California. In comparing the above studies, however, it is important to note that some weed control was used the first couple years of native grass establishment in this and other experiments planting native grasses in the Sacramento Valley, but was not applied in the studies from the other regions.

Table 5. Comparison of mix type invasibility between expected amounts of NNG, had the proportion of each component native species expressed invasibility as it did in monoculture, and actual amounts of NNG.

Treatment	Year	Species	Proportion of Native Species In Mix (%)	Expected Amount of NNG Based on Its Amount in Native Species Monoculture	Actual Amount of NNG in mix
All	2000	EG	24	4%	23
		ET	19	2%	
		HB	13	3%	
		LT	25	2%	
		MC	9	5%	
		NP	11	3%	
		Total		19%	
NP/EG/HB	2000	EG	42	7%	33
		HB	32	8%	
		NP	26	7%	
		Total		22%	
All	2003	EG	14	43 g	243 g
		ET	1	5 g	
		HB	0	1 g	
		LT	71	41 g	
		MC	6	19 g	
		NP	7	22 g	
		Total		131 g	
NP/EG/HB	2003	EG	70	210 g	341 g
		HB	1	4 g	
		NP	29	87 g	
		Total		301 g	
LT/EG	2003	LT	83	50 g	95 g
		EG	17	48 g	
		Total		98 g	
NP/MC	2003	MC	36	107 g	316 g
		NP	64	192 g	
		Total		299 g	

Actual values lower than expected values would indicate that the species-rich mix type was less invasible than each component species in monoculture. EG = *Elymus glaucus*; ET = *Elymus trachycaulus*; HB = *Hordeum brachyantherum*; LT = *Leymus triticoides*; MC = *Melica californica*; NP = *Nassella pulchra*; NNG, non-native grass.

In the Sacramento Valley, studies have found that stands of non-native annual grasses competitively interfere with establishing native grass seedlings (Bartolome & Gemmil 1981; Menke 1992; Dyer et al. 1996, Dyer & Rice 1999; Dyer & Rice 1997; Brown & Rice 2000). Based on the results from the current study, it appears that mature stands of native perennial grasses are able to competitively interfere with establishing annual grass seedlings. Together, these results suggest that priority effects are important in the grassland ecology of this region because the ability of either the native or non-native grass seedlings to establish is substantially hampered by a previously established stand of the other type. Priority effects occur in a system when differences in species arrival order result in community states that differ in species composition or abundance (Belyea & Lancaster 1999; Morin 1999; for review, see Young et al. 2001). In contrast, studies along coastal and southern California suggest that seeded native grasses establishing in an annual-dominated community may have a competitive advantage (Hatch et al. 1999; Seabloom et al. 2003) despite their slower growth.

Species Composition

Species composition played an important role in the extent of invasibility, mostly due to biomass differences, but also due to species effects other than biomass. Among the monospecific plots, the two species with rhizomes, *Leymus triticoides* and *Melica californica*, were the least invasible, although this difference was not significant for *M. californica*. *Leymus triticoides* also had the greatest native biomass, but two other species had greater biomass than *M. californica*. Species with rhizomatous growth may have an advantage over tufted species in resisting invasion by annual grasses because they fill more space in the shallow soil layers. In contrast, the tufted structure of bunchgrasses can create gaps, allowing colonization between the clumps by the shallower rooted annual grasses. Given a native grass community composed of tufted species, overall biomass may be more important than species type in determining competitive ability.

Species Richness and Overyielding

The results from this study do not support the idea that the inclusion of more species in a community necessarily decreases invasion beyond what can be attributed to the proportional contribution of each species acting alone. In other words, there was no evidence of overyielding (or higher order effects) for any mix type having greater than one species in either 2000 or 2003. A rather conservative test of this idea is that the species-rich mixture would be less invasible than the most suppressive species in monoculture. This is similar to transgressive overyielding when productivity is the measured variable (Trenbath 1974). A more liberal test considers whether the diverse mixture is less invasible than the average invasibility of

each component species in monoculture (the “mid-monoculture yield” in productivity experiments) (Trenbath 1974). Again, this was not found to be the case for any mix type having greater than one species in either 2000 or 2003. Studies that include replicated monocultures in their investigations of the relationship between species richness and invasibility have also found that monocultures of the dominant species were less invasible than the species-rich treatments (Palmer & Maurer 1997; Crawley et al. 1999; Dukes 2002). It should be noted that the species-rich treatments used in the current study had both a greater number of species and a greater number of functionally different species.

In experimental systems, attempts are made to control for differences in resources due to extrinsic factors, and it is presumed that variation in resource availability that might affect invaders is the result of competitive interactions among species. Given this reasoning, the results of this and other experiments challenge the idea that multi-species communities necessarily result in greater resource use beyond that of each species in monoculture, or at least use of the resource important to excluding the invader. However, results from the current study do suggest that communities may be less invasible over time by including a diversity of species with different growth rates, however. The ability to resist invasion among species and mixes changed over time. Among the monospecific plots, shorter, slower growing species initially less resistant to invasion had amounts of non-native grass similar to, and in one case less than, the faster growing species by year 5. This is somewhat analogous to Egler's (1954) “initial floristic composition” model, attributing differential growth rates and longevity to the succession of dominant species over time. Perhaps, this characteristic of diverse communities is an important way of deterring invasion by later arriving species. In the mixed-species plots, however, species evenness of native grasses declined, favoring the faster growing more robust species. To maximize community resistance to invasion over time, therefore, the slower growing species might need initial help in reducing competition from faster growing species.

Conclusions and Management Considerations

This study demonstrates that at a site with productive soil and moderate management, mature stands of native grasses may not only obtain greater biomass than non-native annual grasses but also suppress their invasion. These abilities varied with the amount of native grass biomass, species, and time. Mixes with greater species richness did not decrease invasion by non-native grasses. Rather, species traits such as high biomass or rhizomatous growth appear to have been more influential. Because the extent of invasion varied with species over time, restoration projects interested in assessing species performance should consider monitoring for longer than 1–3 years. Further research is needed on the conditions under which

high biomass or levels of native species diversity are achievable and how these qualities relate to multiple restoration and management goals.

Implications for Practice

- Productive stands (>500 g/m) of native grasses in the Sacramento Valley of California can compete with invading non-native annual grasses. Further research into techniques for establishing native grasses from seed should continue.
- Planting a mix of multiple species types does not necessarily result in greater resistance to invasion of the each component species on their own.
- Native grass species with strong rhizomatous growth may be particularly competitive with non-native annual grasses compared with tufted species.
- Despite a lack of direct species richness effects on invasion at any one time, creating opportunities for succession through planting a diversity of species with different growth rates may strengthen resistance of the community to invasion over time.

Acknowledgments

This research was supported with funds from the Experimental Ecosystem, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis. I would like to thank Truman Young, Karen Holl, Kevin Rice, Jan Goerrissen, Jeffrey Corbin, Vicky Temperton, and an anonymous reviewer for valuable comments on the manuscript, and Jan Goerrissen, Michelle Johnson, Tammy Lim, Heidi Kirk, and Danika Tsao for their extensive field assistance.

LITERATURE CITED

- Andrews, W. F. 1990. Soil Survey of Yolo County, California. USDA Natural Resources Conservation Service in cooperation with the University of California Agricultural Experiment Station National Resources Conservation Service, Woodland.
- Bartolome, J. W., and B. Gemmil. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. *Madrono* **28**:172–184.
- Belyea, L. R., and J. Lancaster. 1999. Assembly rules within a contingent ecology. *Oikos* **86**:402–416.
- Borman, M. M., W. C. Krueger, and D. E. Johnson. 1991. Effects of established perennial grasses on yields of associated annual weeds. *Journal of Range Management* **44**:318–322.
- Brown, C. S. 1998. Restoration of California central valley grasslands: applied and theoretical approaches to understanding interactions among prairie species. Ph.D. dissertation. University of California, Davis.
- Brown, C. S., and R. L. Bugg. 2001. Effects of established perennial grasses on introduction of native forbs in California. *Restoration Ecology* **9**:38–48.
- Brown, C. S., and K. J. Rice. 2000. The mark of Zorro: effects of the exotic annual grass *Vulpia myuros* on California native perennial grasses. *Restoration Ecology* **8**:10–17.
- Bugg, R. L., J. H. Anderson, J. W. Menke, K. Crompton, and W. T. Lanini. 1991. Perennial grasses as roadside cover crops to reduce agricultural weeds. *Components: UC Sustainable Agriculture Research and Education* **2**:14–16.
- Bugg, R. L., C. S. Brown, and J. H. Anderson. 1997. Restoring native perennial grasses to rural roadsides in the Sacramento Valley of California: establishment and evaluation. *Restoration Ecology* **5**: 214–228.
- Burcham, L. T. 1957. California range land; an historico-ecological study of the range resource of California. Division of Forestry, Department of Natural Resources, Sacramento.
- Corbin, J. D., and C. M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for a historic species invasion. *Ecology* **85**:1273–1283.
- Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion resistance in experimental grassland communities: species richness or species identity? *Ecology Letters* **2**:140–148.
- Dukes, J. S. 2002. Species composition and diversity affect grassland susceptibility and response to invasion. *Ecological Applications* **12**:602–617.
- Dyer, A. R., H. C. Fossum, and J. W. Menke. 1996. Emergence and survival of *Nassella pulchra* in a California grassland. *Madrono* **43**: 316–333.
- Dyer, A. R., and K. J. Rice. 1997. Intraspecific and diffuse competition: the response of *Nassella pulchra* in a California grassland. *Ecological Applications* **7**:484–492.
- Dyer, A. R., and K. J. Rice. 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* **80**: 2697–2710.
- Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition—a factor in old field vegetation development. *Vegetatio* **4**:412–417.
- Hamilton J. G., J. R. Griffin, and M. R. Stromberg. 2002. Long-term population dynamics of native *Nassella* (Poaceae) bunchgrasses in Central California. *Madrono* **49**:274–284.
- Hatch, D. A., J. W. Bartolome, J. S. Fehmi, and D. S. Hillyard. 1999. Effects of burning and grazing on a coastal California grassland. *Restoration Ecology* **7**:376–381.
- Heady, H. F., J. W. Bartolome, M. D. Pitt, G. D. Savelle, and M. C. Stroud. 1991. California prairie. Pages 313–335 in R. T. Coupland, editor. *Ecosystems of the world, natural grasslands: and Western Hemisphere*, vol. 8, part A. Elsevier, New York.
- Hickman, J. C. 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley.
- Huenneke, L. F. 1989. Distribution of regional patterns of California grasslands. Pages 1–12 in L. F. Huenneke and H. A. Mooney, editors. *Grassland structure and function: California annual grassland*. Kluwer Academic Publishers, Boston.
- Jones, B. J., and R. M. Love. 1945. *Improving California ranges*. Circular 129. California Agricultural Extension Service, University of California, Berkeley.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**:15–26.
- Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**:72–76.
- Mack, R. N. 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. Pages 155–179 in J. A. Drake, H. A. Mooney, F. Dicastri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. *Biological invasion: a global perspective*. John Wiley and Sons, New York.
- Menke, J. W. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia* **20**:22–25.
- Morin, P. J. 1999. Temporal patterns: seasonal dynamics, priority effects, and assembly rules. Pages 235–258 in P. J. Morin, editor. *Community ecology*. Blackwell Science, Oxford, United Kingdom.
- Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. *Endangered ecosystems of the United States: a preliminary assessment of loss and*

- degradation. Biological Report 28. National Biological Service, U.S. Department of the Interior, Washington, D.C.
- Palmer, M. W., and T. A. Maurer. 1997. Does diversity beget diversity? A case study of crops and weeds. *Journal of Vegetation Science* **8**: 235–240.
- Rein, F. A. 1999. Vegetative buffer strips in a Mediterranean climate: potential for protecting soil and water resources. Ph.D. dissertation. University of California, Santa Cruz.
- Richards, R. T., J. C. Chambers, and C. Ross. 1998. Use of native plants on federal lands: policy and practice. *Journal of Range Management* **51**:625–632.
- Sampson, A. W., A. Chase, and D. W. Hedrick. 1951. California grasslands and range forage grasses. Bulletin 724. California Agricultural Experiment Station, University of California, Berkeley.
- SAS Institute Inc. 2002. JMP user's guide, version 5. SAS Institute Inc., Cary.
- Seabloom, E. W., S. W. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences* **100**:13384–13389.
- Stromberg, M. R., and P. Kephart. 1996. Restoring native grasses in California old fields. *Restoration and Management Notes* **14**:102–111.
- Symstad, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* **81**:99–109.
- Trenbath, B. R. 1974. Biomass productivity of mixtures. Pages 177–210 in N. C. Brady, editor. *Advances in agronomy*, vol. 26. Academic Press, New York.
- Troumbis, A. Y., A. Galanidis, and G. D. Kokkoris. 2002. Components of short-term invasibility in experimental Mediterranean grasslands. *Oikos* **98**:239–250.
- Van Ruijven, J., G. B. De Deyn, and F. Berendse. 2003. Diversity reduces invasibility in experimental plant communities: the role of plant species. *Ecology Letters* **6**:910–918.
- Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility—evidence of a biological mechanism or a consequence of sampling effect? *Oikos* **95**:161–170.
- White, K. L. 1967. Native bunchgrass (*Stipa pulchra*) on Hastings Reservation, California. *Ecology* **48**:949–955.
- Young, T. P., J. M. Chase, and R. T. Huddleston. 2001. Community succession and assembly. *Ecological Restoration* **19**:5–18.