

COMPETITION BETWEEN NATIVE PERENNIAL AND EXOTIC ANNUAL GRASSES: IMPLICATIONS FOR AN HISTORICAL INVASION

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Abstract. Though established populations of invasive species can exert substantial competitive effects on native populations, exotic propagules may require disturbances that decrease competitive interference by resident species in order to become established. We compared the relative competitiveness of native perennial and exotic annual grasses in a California coastal prairie grassland to test whether the introduction of exotic propagules to coastal grasslands in the 19th century was likely to have been sufficient to shift community composition from native perennial to exotic annual grasses. Under experimental field conditions, we compared the aboveground productivity of native species alone to native species competing with exotics, and exotic species alone to exotic species competing with natives. Over the course of the four-year experiment, native grasses became increasingly dominant in the mixed-assemblage plots containing natives and exotics. Although the competitive interactions in the first growing season favored the exotics, over time the native grasses significantly reduced the productivity of exotic grasses. The number of exotic seedlings emerging and the biomass of dicot seedlings removed during weeding were also significantly lower in plots containing natives as compared to plots that did not contain natives. We found evidence that the ability of established native perennial species to limit space available for exotic annual seeds to germinate and to limit the light available to exotic seedlings reduced exotic productivity and shifted competitive interactions in favor of the natives. If interactions between native perennial and exotic annual grasses follow a similar pattern in other coastal grassland habitats, then the introduction of exotic grass propagules alone without changes in land use or climate, or both, was likely insufficient to convert the region's grasslands.

Key words: *California grassland; coastal prairie grassland; exotic annual grasses; grass competition; invasive species; native perennial grasses; priority effects.*

INTRODUCTION

Biotic invasions have been recognized as a major component of human-caused global change (Williamson 1996, Vitousek et al. 1997a), particularly in cases where invasions have resulted in the disruption of entire ecosystems by altering community composition, nutrient cycling rates, or disturbance regimes (Vitousek et al. 1987, 1997b, D'Antonio and Vitousek 1992). Considerable theoretical and experimental effort has been dedicated to identifying the factors that contribute to the success of exotic species in habitats where they have been introduced or are spreading (Reichard and Hamilton 1997, Lonsdale 1999, Mack et al. 2000). Though generalized principles that govern the probability of invasion success across habitat types remain elusive, understanding interactions between invaders and residents is essential to the management and restoration of native-dominated habitats.

A recent review of competitive interactions between native and exotic plants suggested that the ability of

the exotic species to establish and spread is related to their ability to competitively suppress resident species (Levine et al. 2003). Invasions, however, are also known to be facilitated by disturbances that create gaps in vegetation cover such as grazing, gopher activity, or fires (Crawley 1987, Hobbs 1989, Hobbs and Huenneke 1992, Burke and Grime 1996). In these cases, exotic species may successfully establish only when disturbances decrease the competitive interference or priority effects (*sensu* Paine 1977) of resident vegetation. The degree to which the success of an invasion is explained by competitive superiority on the part of the exotic species vs. disturbances that allow exotics to become established is important to the design of strategies to control invaders.

The conversion of California grasslands from ecosystems dominated by indigenous perennial grass and annual and perennial dicot species to ecosystems dominated by Eurasian annual species is one of the best-known examples of large-scale community change occurring in North America over the past two centuries (Mack 1989), yet little is known about what factors contributed to the success of the Eurasian invaders. The introduction of Eurasian species to California grasslands coincided with other dramatic changes in the en-

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vironment, including widespread tilling associated with agriculture, the addition of millions of livestock, and a severe drought during the mid-19th century (Burcham 1957, Major 1988, Stromberg and Griffin 1996). While these changes in land use and climatic conditions almost certainly increased the likelihood that the exotic species would become established, it is not known whether they were necessary components of the invasion process.

Grasslands in California are typically divided into two large-scale habitat types that differ in climatic conditions and species composition. Interior grasslands, or valley grasslands (*sensu* Heady 1988) occupy the hot and dry regions of the Coast Range, Central Valley, and Sierra Nevada foothills and are largely dominated by exotic annual grasses and forbs along with remnant native perennial grasses such as *Nassella pulchra* A. Hitchcock (Barkworth). Coastal prairie grasslands, which occur within 100 km of the coast, experience milder summertime climatic conditions due to maritime influences and to this day, perennial grasses codominate many habitats (Elliott and Wehausen 1974, Heady et al. 1988, Peart 1989a, Stromberg et al. 2001). It is possible that different factors contributed to the success of the exotic species in each habitat type. Evidence from Central Valley grasslands and other interior regions of the state, that exotic species competitively suppress native species (e.g., Dyer and Rice 1997, Hamilton et al. 1999, Brown and Rice 2000), has led to the hypothesis that once seeds of exotic species were introduced, the shift in community composition toward exotic species would have proceeded regardless of any changes in land use or climatic conditions (Bartolome and Gemmill 1981, Heady 1988, Murphy and Ehrlich 1989). In coastal habitats, however, the native perennial grasses may have been superior competitors to the introduced annual species. The conversion of coastal prairie grassland ecosystems from native-perennial dominated to exotic-annual dominated ones may have required some sort of widespread disturbance or stress.

We compared these alternative hypotheses by testing competitive interactions between native and exotic grasses in a coastal prairie grassland ecosystem in northern California. Native perennial grasses were planted as three-month-old seedlings, and we focused our comparisons on the impacts of exotic grasses on relatively established native individuals rather than the establishment of natives from seed. We compared the aboveground productivity of native species alone to native species competing with exotics, and exotic species alone to exotics competing with natives. Evidence that the exotic grasses were able to consistently reduce the growth or survival of native grasses would support the hypothesis that the introduction of exotic propagules in the 19th century was sufficient to cause the compositional shift of California coastal prairie grasslands. On the other hand, evidence that native perennial grasses were strongly competitive, particularly as they

became established, would suggest that disturbances such as agriculture, grazing, or severe drought conditions were likely important factors in the compositional shift.

METHODS

Study area

We established our experimental plots at Tom's Point Preserve, a private nature preserve adjacent to Tomales Bay in Marin County, USA (38°13' N, 122°57' W; Appendix A). Livestock grazing has not occurred in the preserve for at least 30 years. The portion of the preserve in which we established our plots was dominated by introduced annual grasses including *Avena barbata* Link., *Bromus diandrus* Roth, and *Vulpia myuros* (L.) C. Gmelin, introduced perennial grasses including *Festuca arundinacea* Schreber and *Holcus lanatus* L., and such exotic annual and biennial forbs as *Carduus pycnocephala* L. and *Conium maculatum* L. Nomenclature follows Hickman (1993). Few native grasses were present where we established our plots, though they were abundant in other areas of the preserve. The soil at the study site was a sandy loam (fine, mixed mesic Ultic Paleustalf).

The climate at Tom's Point is typical of California's mediterranean seasonality, with most of the precipitation falling between November and April (Fig. 1). Coastal fog, present in the summer months, moderates the summer drought (Ingraham and Matthews 1995, Dawson 1998; J. D. Carbin, M. A. Thomsen, T. E. Dawson, and C. M. D'Antonio, *unpublished manuscript*). Germination of annual species is generally stimulated by the first significant (>15 mm) rainfall event in the fall. Peak growth for annual species is generally in late February through the end of March. For perennial species, peak growth extends further into the spring and early summer.

Experimental design

In September 1998 standing vegetation was cut and sprayed with 5–10% glyphosate-based herbicide. All biomass and litter were removed, leaving bare soil. We established eight replicates of each of three different community types in a randomized block design (two blocks): native perennial bunchgrasses only (N), exotic annual grasses only (E), and natives and exotics together (N + E). Each of the 24 plots was 1.5 × 1.5 m with a 1–2 m buffer between plots. Seeds of the exotic annual grasses *A. barbata*, *B. diandrus*, and *V. myuros* were cast onto E and N + E plots in early December 1998. Seed densities were chosen to fall within the range reported by Heady (1958) for California annual grasslands: *A. barbata* = 3400 seeds per plot, *B. diandrus* = 1750 seeds per plot, and *V. myuros* = 9000 seeds per plot. In subsequent years, annual seeds were reapplied both by allowing established plants from the previous growing season to set seed and by supple-

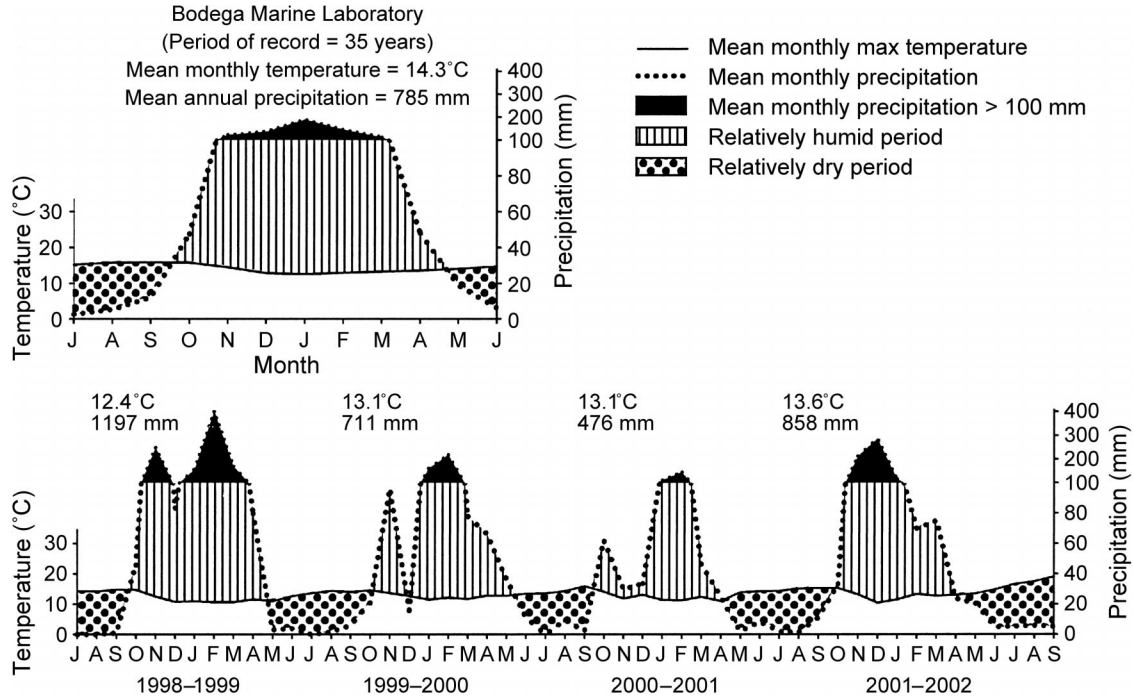


FIG. 1. A 35-year average Walter climate diagram and four consecutive one-year Walter climate diagrams for Bodega Marine Laboratory, 20 km north of Tom's Point Preserve (see Walter [1985] for further explanation). The values for the four separate years are mean monthly temperature and total precipitation. Note the change in scale of the y-axis >100 mm precipitation. Data are courtesy of Bodega Marine Laboratory, University of California, Davis.

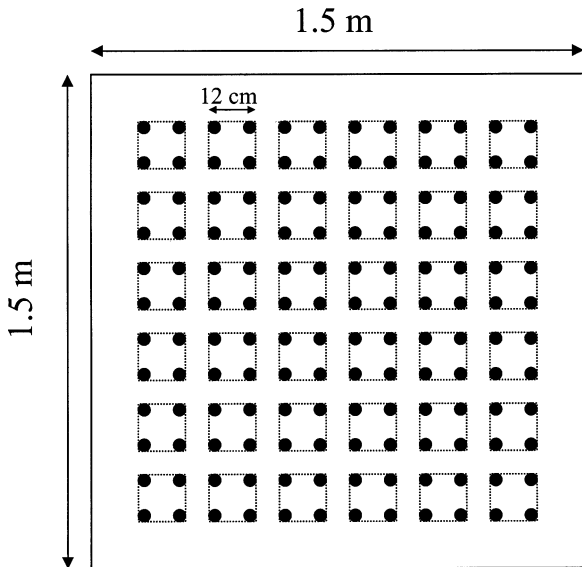


FIG. 2. Diagram of the arrangement of native perennial grasses in each plot. Each point represents a single native plant, separated from its neighbor by 12 cm. Plants were grouped by species in "neighborhoods" of two plants × two plants, represented by the dotted squares. There were a total of 36 neighborhoods and 144 individual plants in each 2.25-m² plot.

menting this natural seed rain with seed collected from outside the experimental plots. We expected that this augmentation of the natural seed rain would eliminate any difference in annual seed availability between treatments due to competitive effects. Seeds were added at similar levels as the first season, with the exception that the number of *V. myuros* seeds was reduced to 7750 seeds per plot. All seeds were collected at Tom's Point the spring prior to planting and stored at room temperature. No pregermination treatments were applied to the seeds, as these species have been shown to exhibit high rates of germination under these conditions (Reynolds et al. 2001).

Seeds of the native perennial grasses *Agrostis oregonensis* Vasey, *Festuca rubra* L., and *N. pulchra* were collected by hand at Tom's Point in spring 1998. Seeds were planted in individual Containers (Stuwe and Sons, Corvallis, Oregon, USA) in September 1998 and allowed to germinate under greenhouse conditions. The three-month-old seedlings were transplanted into N and N + E plots during 5–14 January 1999 at a density of 144 plants per plot. Each plant was separated from its neighbors by 12 cm within a 12 × 12 plant grid. Within a plot, the seedlings were organized into "species neighborhoods" made up of four plants of the same species (36 groups per plot; Fig. 2). Location of the neighborhoods in each plot was random, though the placement was constrained so that each species had at least one neighborhood in the central 1 m² of each grid.

Mean biomass of each species at the time of planting, determined by harvesting, drying, and weighing 20 randomly selected individuals of each species, was 0.074 ± 0.008 g, mean ± 1 SE, 0.055 ± 0.006 g, and 0.044 ± 0.004 for *N. pulchra*, *A. oregonensis*, and *F. rubra*, respectively. Dead individuals were replaced for the first month, but perennial seedling survival after transplanting was very high (>99% for all species).

Plots were weeded of dicots and nontarget grasses three times each year to maintain species composition and density. We collected all dicots weeded out of the plots in 2000–2001 (December, January, and March), and separated them by plot. Though we did not record species composition, the exotic forbs *Rumex acetocella* L., *C. pycnocephala* and *C. maculatum*, and the native annual forb *Eschscholzia californica* (Cham.) were the most abundant species.

Plant growth and reproductive production

Aboveground biomass, including vegetative and reproductive tissue, of exotic grasses was destructively harvested in either late May or June of each season, depending on the timing of peak biomass for the vegetation. All aboveground biomass was clipped to ground level in three randomly selected 0.25×0.25 m subsamples in each plot and separated by species. This harvest accurately reflects total aboveground productivity, because exotic annual grasses die back completely each spring. Following drying (60°C) to constant mass, each sample was weighed and returned to appropriate plots.

The number of emerged exotic seedlings was estimated by counting all seedlings in four randomly located 10×10 cm subplots in each E and N + E plot on 29 January 2000. It was assumed that the counts accurately reflected germinated seeds before seedling mortality would have taken place.

Aboveground biomass of native grasses was sampled nondestructively to minimize disturbance. We constructed allometric relationships between basal diameter, longest leaf length, and the number of flowering culms and the aboveground biomass for each species by harvesting 76–87 individuals of each species (Appendix B). Relationships were found to vary over time, so separate regressions were performed for the first sample date (March 1999) and all subsequent sample dates. The r^2 of the allometric equations for each species was >0.85 . Natives were measured twice per season to estimate annual productivity (Appendix C).

Reproductive output of perennials was estimated in June 2001 by harvesting inflorescences of three randomly selected individuals of each species in each plot. Seeds of all species except *N. pulchra* were dried (60°C) to constant mass and weighed. Because of its earlier flowering time, many *N. pulchra* seeds had already matured and dropped. *Nassella pulchra* inflorescences have one floret per spikelet, so the number of

seeds per plant was estimated by counting the number of spikelets.

Light levels

Quantum light levels were measured in each plot in order to estimate photosynthetically active light reaching the soil surface. Three randomly selected points in each plot were sampled 1 cm above the soil surface using a LI-COR LI-189 quantum light meter (LI-COR, Lincoln, Nebraska, USA). Each measurement was standardized as a percentage of full sunlight to produce an estimate of percentage of sunlight reaching below the canopy. Sampling was performed in January, March, and June 2003, the fifth year of the experiment.

Statistical analyses

The responses of vegetation productivity to competition (annuals on perennials, and perennials on annuals) were tested using repeated-measures ANOVA (SAS Institute 2000). The model used included Block, Competition, Year, and the interaction between Year and Competition. The effects of Year and the Year \times Competition interactions were analyzed with MANOVA using Roy's Greatest Root (Scheiner 1993). Linear contrasts between Year and Competition were also constructed to test whether there was a trend in the response of native or exotic vegetation over the course of the experiment. Separate ANOVAs were run for each year's vegetative productivity to test the impact of competition each year, since repeated-measures analysis indicated significant Time \times Competition interactions in nearly all cases. Native biomass in June 2002 was also analyzed using ANOVA. All variables were log-transformed to meet the assumptions of ANOVA.

Weeded forb biomass, and the number of emerged annual seedlings were analyzed using ANOVAs in which Block and Treatment were dependent variables. When analysis indicated a significant main effect of Treatment, Bonferroni-corrected pair wise comparisons were performed. Quantum light levels were analyzed using repeated-measures ANOVA, following arcsin-transformation.

We calculated a correlation coefficient for the relationship between native perennial and exotic annual aboveground productivity over the four years of the study. Because plots were sampled repeatedly, assumptions of independence required for hypothesis testing were not valid, though such assumptions are not necessary to compute a correlation coefficient (Zar 1996).

RESULTS

Weather patterns

Precipitation at Bodega Marine Laboratory, 20 km north of Tom's Point, varied during the four-year experiment, as the annual precipitation (July–June) was higher than the 35-year average in the first and fourth

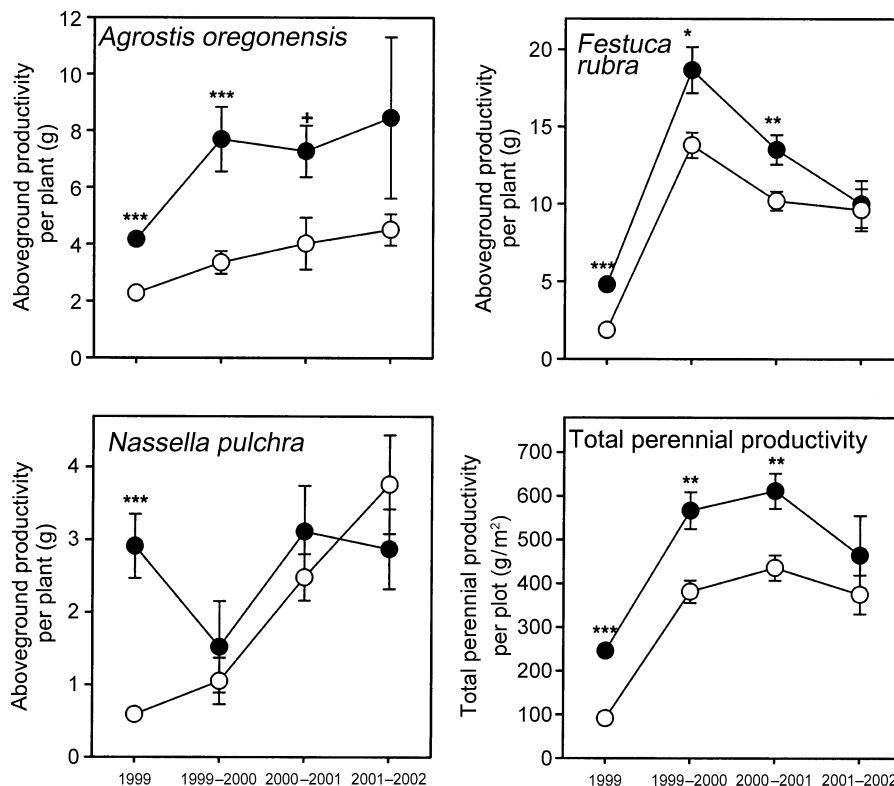


FIG. 3. Mean productivity (± 1 SE) of each native perennial bunchgrass and total native productivity from 1998 to 2002. Descriptions of treatments are given in the *Methods*. Key to symbols: solid circles, no exotic competitors (N); open circles, with exotic competitors (N + E). Asterisks indicate statistical significance between treatments in a given year: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; +, $0.05 < P < 0.1$. *F* statistics and results of repeated-measures ANOVA are presented in Appendix D.

seasons, and lower than the average in the second and third seasons (Fig. 1). The 1999–2000 and 2000–2001 seasons were also characterized by mid-growing season droughts in which monthly precipitation (December–January) was < 35 mm. Mean annual temperature was relatively consistent about the 35-year average.

Vegetation productivity

The effect of the exotics on native productivity decreased over the course of the experiment, as natives comprised greater and greater proportions of the biomass in mixed-assemblage plots (N + E). Total native productivity in N plots was more than 2.5 times greater than in N + E plots in the first growing season, but by 2001–2002 there was no significant difference between the treatments (Fig. 3; Appendix D). Linear contrasts between Year and Competition indicated that the difference between N and N + E decreased over the four-year period in the cases of total native productivity and the productivity of two of the native species, *Festuca rubra* and *Nassella pulchra*. Though the overall productivity by native species was smaller in N + E plots than in N plots (repeated-measures ANOVA: Appendix D), the aboveground biomass of *F. rubra* and *N. pulchra* individuals at the end of the fourth growing season

did not differ between treatments (Fig. 4). Competition with exotic competitors had the least impact on *N. pulchra* of all the natives, though *N. pulchra* was consistently the smallest and least productive of the native perennial grasses (Figs. 3 and 4).

We also measured native performance using reproductive output and survival at the end of the third growing season, 2000–2001. Seed production by natives was not significantly different in N plots as compared to N + E plots (Table 1). Survival of natives through the end of the third growing season was high in both N and N + E treatments. No *F. rubra* individuals died in the entire experiment, while only two *Agrostis oregonensis* individuals died, one each in a plot with exotic competitors and a plot without exotic competitors. Mean survival of *N. pulchra* individuals was $91 \pm 0.03\%$, mean ± 1 SE, (SE = 0.03) and $86 \pm 0.08\%$ in plots with and without exotics, respectively. This difference was not significant.

Exotics were significantly negatively affected by competition with native species, as overall productivity by exotic species was significantly lower in N + E plots as compared to E plots (Fig. 5; repeated-measures ANOVA: Appendix D). In 1998–1999, the aboveground biomass of the exotics either did not differ be-

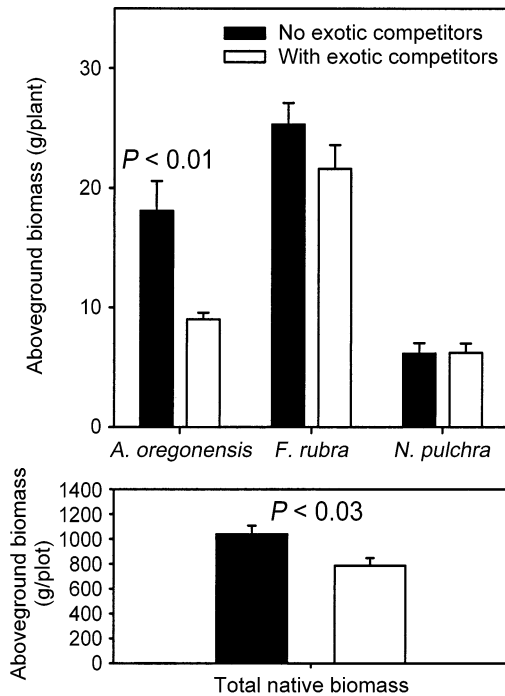


FIG. 4. Mean biomass (± 1 SE) of each native perennial bunchgrass and total native biomass in June 2002. Significant differences between treatments within a species are indicated by P values based on ANOVA tests of within-year effects.

tween the E and N + E treatments or, in the case of *Avena barbata*, was slightly lower in E treatments than in N + E treatments. In each of the subsequent three years, total exotic productivity was 2–5 times greater in E plots than in N + E plots (Fig. 5; Appendix D). The difference in productivity between E and N + E plots increased over the four-year period in the cases of *A. barbata* and *Vulpia myuros*, and the total exotic productivity (linear contrasts: Appendix D).

Over the course of the four-year experiment, natives became increasingly dominant in the mixed-assemblage plots (N + E). The exotic grasses' proportion of the total productivity in N + E plots declined from 45.7% in 1998–1999, to 6.4%, 3.4%, and 5.4% in subsequent years. Exotic productivity in these plots was negatively correlated with native productivity ($r = -0.74$; Fig. 6), and significantly fewer exotic seedlings emerged in N + E plots as compared to E plots in winter 2001 (Table

2). Plots containing natives (N and N + E plots) also had significantly lower dicot biomass removed during weeding as compared to E plots (Table 2).

Light levels

Light levels between January and June 2003 were significantly lower in N and N + E plots as compared to E plots (Fig. 7; repeated-measures ANOVA: treatment, $F_{2,17} = 27.3$, $P < 0.0001$). Though light levels decreased significantly over the course of the season (time, $F_{2,16} = 14.9$, $P < 0.0002$), there was no significant interaction between treatment and time.

DISCUSSION

Native perennial bunchgrasses were strongly competitive with exotic annual grasses in this coastal prairie ecosystem. In the first growing season, the presence of exotics significantly reduced native productivity, while exotic productivity was unaffected by the presence of natives. In subsequent seasons, however, the native grasses significantly reduced the productivity of exotic grasses while the negative effect of exotics on native productivity became smaller and smaller. Despite the repeated addition of more than 5600 exotic seeds·m⁻²·yr⁻¹, native species came to occupy larger and larger proportions of the N + E plots. By the end of the four-year experiment, the effect of exotic competitors was detectable on the aboveground biomass of only one of the three native species, *A. oregonensis*. For *F. rubra* and *N. pulchra*, there was no legacy of the first-year effect of exotic competitors, as by the fourth year, the biomass of individuals in the N + E plots was not significantly smaller than individuals in the N plots. There was also no detectable effect of exotics on native mortality or reproductive output.

We conclude that the introduction of exotic annual propagules is not likely to have been sufficient by itself to precipitate the dramatic shift in grassland composition that occurred in many coastal California ecosystems. Within 1–2 years after establishment, native perennial bunchgrasses in our experiment were capable of substantially reducing exotic productivity and the productivity of weedy dicots entering from outside our plots. Indeed, established stands of native perennial grasses such as those that exotic propagules would have encountered in the 19th century would likely have exerted an even stronger effect on exotic grass produc-

TABLE 1. ANOVA of the effects of treatment on seed production (mean ± 1 SE) by each native perennial grass in 2000–2001.

Species	N	N+E	F	P
<i>Agrostis</i> †	0.68 \pm 0.21	0.28 \pm 0.07	1.1	0.4
<i>Festuca</i> †	2.09 \pm 0.61	1.58 \pm 0.34	0.1	0.8
<i>Nassella</i> ‡	229.25 \pm 46.19	147.75 \pm 42.15	2.6	0.2

Note: Treatment abbreviations are: N, native only; N+E, native + exotic.

† Seed mass (g/3 individuals).

‡ Seed number (seeds or spikelets/3 individuals).

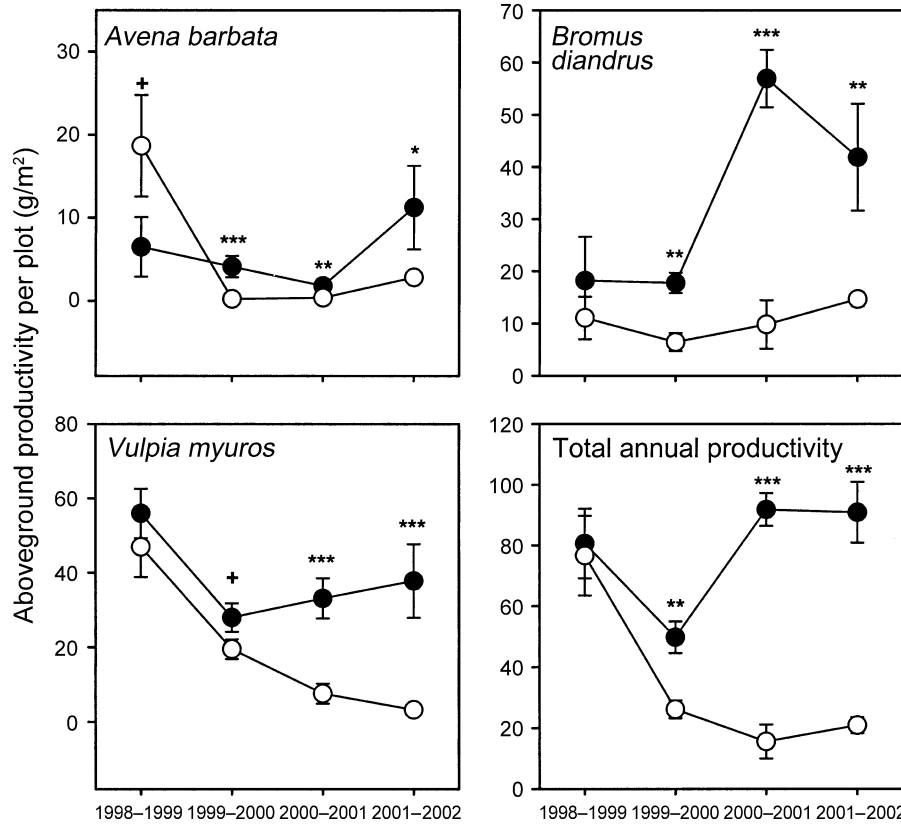


FIG. 5. Mean productivity (± 1 SE) of each exotic annual grass and total exotic productivity from 1998 to 2002. Key to symbols: solid circles, no native competitors (E); open circles, with native competitors (N + E). Significance labels are as in Fig. 3.

tivity than our newly planted native communities. Instead, disturbances associated with European settlement or adverse climatic conditions, or both, were likely essential components of the widespread grassland conversion. Scattered remnant patches of native-dom-

inated grassland in coastal California, in which exotic cover can be <10% (Heady et al. 1988, Stromberg et al. 2001; Appendix A) illustrate that under certain conditions native species are capable of resisting conversion to exotic dominance.

It is possible that the invasion of exotic annual grasses in the 19th century reduced the ability of native grasses to colonize natural disturbances enough so that native populations were unable to replace themselves. A variety of studies have demonstrated that exotics reduce *N. pulchra* seedling establishment (Dyer et al. 1996, Hamilton 1999), and that exotic annual grasses are more successful at colonizing gopher mounds than are native perennial grasses (e.g., Peart 1989c, Hobbs and Mooney 1991, Stromberg and Griffin 1996). However, Peart (1989c) reported that, while the exotic annual grass *V. myuros* was a better colonizer of coastal prairie canopy openings and gopher mounds in the first year than were four perennial bunchgrasses, the perennial bunchgrasses replaced *V. myuros* in the second year. We suspect that the impact of exotic annual grasses on native regeneration may have contributed to the conversion of California coastal prairie grasslands and has likely been a key impediment to the recovery of native perennial grass populations. However, further study would be necessary to determine whether the ability of exotics to colonize

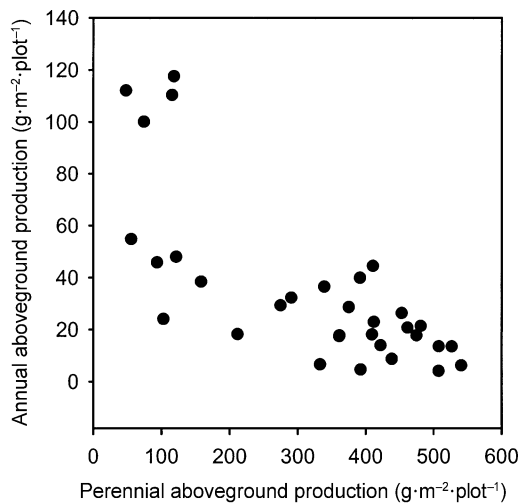


FIG. 6. Correlation between aboveground productivity of exotic annuals and native perennials in N + E plots during the four-year experiment; $r = -0.74$.

TABLE 2. ANOVA of the effects of treatment on emerged annual seedlings and biomass of weeded dicots (mean \pm 1 SE).

Variable	N	E	N+E	F	df	P
Emerged annual seedlings [†]		272 ^b \pm 25	55 ^a \pm 12	55.3	1, 13	0.0001
Dicot biomass (g/m ²)	11.6 ^a \pm 1.8	29.2 ^b \pm 6.6	13.3 ^a \pm 4.0	6.7	2, 20	0.007

Notes: Treatment abbreviations are: N, native only; E, exotic only; N+E, native + exotic. Treatment means with different letters (a, b, c) in each row are significantly different from each other. See *Methods* for details.

[†] Number of seedlings/0.04 m².

natural disturbances played as important a role in the conversion of coastal California grasslands as the anthropogenic disturbances and adverse climatic conditions of the 19th century.

The strong competitiveness of the established natives relative to the exotics emphasizes the importance of disturbances in reducing community resistance to invasion (Hobbs and Huenneke 1992, Mack et al. 2000). By disrupting the priority effects of well-established residents, disturbances, whether at large or small scales, can increase resource availability to the advantage of fast-growing invaders (D'Antonio et al. 1999, Davis et al. 2000). Many disturbances, such as gopher activity, are a regular feature of herbaceous vegetation. Hence, an essential future step is to identify the extent to which small-scale disturbances by native animals alone or in combination with stresses such as drought (Hamilton et al. 1999) can disrupt priority effects and eventually lead to the conversion of native-dominated vegetation. Such knowledge could help to identify time windows in which plant communities are vulnerable to rapid change.

Mechanisms of competition between native perennial and exotic annual species

Differences in life history traits between the species groups may provide advantages to the native perennial

bunchgrasses competing with exotic annual grasses in California coastal prairies. California cool-season annual species, including the exotic annual grasses, germinate from seed in the fall and complete their growth and reproduction by the following spring. They produce seeds that delay germination through the summer drought period until the next fall's rains. In contrast, native perennial bunchgrasses maintain above- and belowground tissue throughout the summer drought period (Jackson and Roy 1986, Holmes and Rice 1996). An established perennial individual would be expected to have primary access to such resources as soil nutrients, water, and light, and could limit available space for germinating annual seeds. Each fall, established perennial individuals in coastal prairie grasslands may enjoy advantages of being "incumbents" in the community and have a negative effect on annual species that must germinate from seed. The shift in competitive interactions in favor of the established perennial individuals may be an example of priority effects (Paine 1977), whereby earlier arriving individuals are able to preempt resources or space (Ross and Harper 1972, Peart and Foin 1985, Quinn and Robinson 1987, D'Antonio et al. 2001).

We did find evidence of priority effects in that in the third growing season, natives reduced the density of

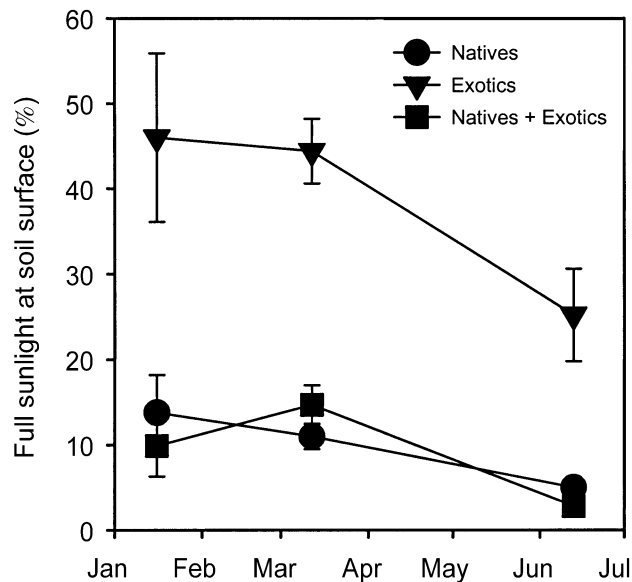


FIG. 7. Quantum light levels (\pm 1 SE), standardized as a percentage of full sunlight, reaching the soil surface in each treatment in 2003. Repeated-measures ANOVA indicated that the effects of treatment and time were significant (see *Methods* for details).

emerging exotic seedlings and reduced the availability of light to the exotics. We believe that the ability of the established native perennial grasses to limit the space available for exotic annual seeds to germinate and to limit the light available to exotics reduced exotic productivity and shifted competitive interactions in favor of the natives.

Comparisons between our study in a coastal prairie grassland and ones in interior grasslands suggest that competitive interactions between exotic annual grasses and native perennial bunchgrasses vary across grasslands within California. Exotic annual grasses have been shown to reduce growth and reproductive output of *N. pulchra* seedlings and adults in the Central Valley (Dyer and Rice 1997, Brown and Rice 2000), the San Ynez Valley of California (Hamilton et al. 1999), and in interior Coast Range valleys (Bartolome and Gemmill 1981). The exotics have also been shown to be superior competitors for light and water as compared to *N. pulchra* seedlings (Dyer and Rice 1999, Hamilton et al. 1999) and adults (Hamilton et al. 1999). *Nassella pulchra* has not been previously shown to have the capacity to reduce exotic annual grass productivity (e.g., Hamilton et al. 1999).

The coastal California environment in which our experiment took place differed in a number of important ways from previous comparisons between native and exotic grasses. In the context of grasslands throughout the state, our sites were within the large coast range environment where the summer drought is moderated by maritime influences. It is likely that experimental results would be different in drier interior valleys and Sierra Nevada foothills.

Patterns of precipitation or temperature in particular seasons are known to influence grassland composition and diversity in California (Heady 1988), and the results of interactions between native perennial and exotic annual grass species likely vary with weather patterns. Yet, natives reduced exotic productivity in both relatively wet (year 4) and relatively dry (year 3) years, indicating that our results were not dependent on extreme weather conditions. It is unknown what impact the 1–2 month periods of relative drought that took place during the 1999–2000 and 2000–2001 growing seasons had on the competitive interactions. Hamilton et al. (1999) simulated a 35-day drought early in the growing season, and concluded that negative effects of the drought on exotic annual grasses indirectly benefited *N. pulchra* seedlings. The established perennial grasses in our study, with their established root systems, may have had an even greater advantage over annual grasses during the midseason drought periods.

Species composition and community diversity have also been shown to have important influences on the outcome of invasion studies (Tilman 1997, Levine and D'Antonio 1999, Levine 2000), and the presence of two additional native species in the species pool in our experiment likely had an important effect on competitive

suppression of the exotic annuals by the native perennials. Virtually all other studies of the interaction of native and exotic annual species in California use *N. pulchra* as the native species. Though *N. pulchra* was one of the species included in our mixture of perennial species, it was consistently the smallest of the three. Hence, our inclusion of three, rather than only one, native species could be partially responsible for differences between ours and other studies.

The pattern of the increasing competitiveness of perennial species in comparison to exotic annual species in our site resembles succession from winter annual species to biennial and perennial herbaceous species in old-field succession (e.g., Keever 1950, Bazzaz 1968, Meiners et al. 2002). Yet, exotic annual grasses in California are notable in their resistance to successional change once they are well established (Bartolome and Gemmill 1981, Stromberg and Griffin 1996). Given that established perennial grasses can be strongly competitive and are capable of suppressing exotic annual grasses, the question remains as to how the exotic species have been able to maintain their dominance in many coastal prairie grasslands. The exotic annual grasses likely benefit from anthropogenic disturbances such as earthmoving activities and livestock grazing (Stromberg and Griffin 1996) as well as natural disturbances such as fossorial mammal activities (Peart 1989c, Dyer et al. 1996, Stromberg and Griffin 1996, Schiffman 1997) that are important features of many grassland ecosystems. There is also evidence that recruitment of native perennial grass seedlings is low even in grasslands where natives persist, and that establishment may be limited by low seed production or availability of propagules from source populations (Bartolome and Gemmill 1981, Peart 1989a, Dyer et al. 1996, Hamilton et al. 1999, Seabloom et al. 2003). Native perennial grass populations may resemble populations of other grazing-sensitive species that are slow to recover after the cessation of grazing (Watt 1957). It is also possible that changes in mycorrhizal community composition as the plant community has shifted from native- to exotic-dominated has altered vegetation–microbial associations (Kourtev et al. 2002). Finally, although established native grasses are successful competitors and can survive for many years, native seedlings have been shown to suffer high rates of mortality in the dense stands created by exotic annual seedlings (Bartolome and Gemmill 1981, Peart 1989b, Dyer and Rice 1997, Hamilton et al. 1999, Brown and Rice 2000). Thus, the failure of native perennial grasses to reenter areas now dominated by exotic grasses may primarily be due to low probability of seedling establishment.

CONCLUSIONS

Though exotic annual grasses in our experiment initially suppressed native grasses, in subsequent years native perennial grasses were the superior competitors. If interactions between the two species groups follow a similar pattern in other coastal grassland habitats, then

the introduction of exotic grass propagules alone without changes in land use or climate, or both, was likely insufficient to convert the coastal California grasslands from native perennial-dominated to exotic annual-dominated grasslands. We believe that the strong competitiveness of established native perennial species in our study indicates that exotic annual- and native perennial-dominated grasslands may represent alternative vegetation states that are both capable of persisting in coastal prairie habitats. Such a finding offers hope that efforts to restore native components of degraded California grasslands have a high probability of success as long as native perennial grass seedlings are able to survive the earliest stages of establishment.

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APPENDIX A

A photograph showing native perennial-dominated coastal prairie grassland at Tom's Point Preserve, Marin County, California, USA is available in ESA's Electronic Data Archive: *Ecological Archives* E085-033-A1.

APPENDIX B

A description of the allometric relationships between size and biomass for each native perennial species is available in ESA's Electronic Data Archive: *Ecological Archives* E085-033-A2.

APPENDIX C

A description of the measurement of native perennial productivity is available in ESA's Electronic Data Archive: *Ecological Archives* E085-033-A3.

APPENDIX D

A table showing repeated-measures ANOVA and single season ANOVAs for the effects of the intergroup competition on productivity of native perennials and exotic annuals is available in ESA's Electronic Data Archive: *Ecological Archives* E085-033-A4.