



Mechanisms of resistance to invasion in a California grassland: the roles of competitor identity, resource availability, and environmental gradients

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Resistance to the invasion of exotic plants may sometimes result from the strong effects of a relatively small number of resident species. Understanding the mechanisms by which such species resist invasion could provide important insights for the management of invaded ecosystems. Furthermore, the individualistic responses of community members to resource availability and environmental gradients could drive spatial variation in resistance at the local to landscape scales. We tested the resistance of monoculture plots of three native perennial grasses from the California coastal prairie to the invasion of the European perennial grass *Holcus lanatus*. We also used a watering treatment that increased early summer water availability and a natural elevational gradient in resource availability and soil texture to evaluate how resident identity interacted with abiotic resistance to affect *Holcus* establishment. Two native species, *Festuca rubra* and *Calamagrostis nutkaensis*, exhibited strong resistance, correlated with their negative effects on light availability. A third native grass, *Bromus carinatus* var. *maritimus*, had either no effect or a weakly facultative effect on *Holcus* performance relative to bare plots. Water addition did not alter the resistance of these species, but the elevation gradient did. *Holcus* invasion increased with improving abiotic conditions towards the slope bottom in bare and *Bromus* plots, but invasion decreased towards the bottom in *Calamagrostis* plots, where better conditions favored competitive residents. These results support the idea that resistance to invasion can sometimes be due to a subset of native species, and that the resistance provided by even a single species is likely to vary across the landscape. Identifying the mechanisms by which species resist invasion could facilitate the selection of management strategies that at best increase, or at worst do not decrease, natural resistance.

Invasive exotic plant species have caused alterations in the species diversity, ecosystem functioning, and aesthetic value of many habitats around the world (Lonsdale 1999, Mack 2000, Levine et al. 2003). In other habitats, however, the same exotic species may be unable to establish, or may persist as only a minor component of the vegetation (Alpert et al. 2000, Mack et al. 2000, Tilman 2004). The characteristics that slow down or prevent the establishment of an exotic species comprise a site's resistance to invasion (Elton 1958, D'Antonio et al. 2001); those that facilitate establishment and spread contribute to the habitat's invasibility (Lonsdale 1999). An understanding of the processes contributing to resistance and to invasi-

bility can assist in the management of uninvaded habitats, or the restoration of sites so as to reduce their susceptibility to future encroachment of unwanted species (D'Antonio and Thomsen 2004, Fargione and Tilman 2005).

The hypothesized positive relationship between species diversity and invasion resistance has been a major focus of ecological research (Elton 1958, Levine 2000, Naeem et al. 2000, Prieur-Richard 2002, Fargione and Tilman 2005), although the opposite pattern has also been documented, especially at larger spatial scales (Rejmanek 1996, Stohlgren et al. 1999, Davies et al. 2005). The greater local-scale resistance of diverse communities is thought to result from two

mechanisms involving competition. First, resources may be more fully utilized in diverse communities because of niche complementarity among coexisting species, resulting in lower resource availability for invaders (Hooper 1998, Naeem et al. 2000, Fargione and Tilman 2005). Alternatively, the lower invasibility of diverse communities could result from a “sampling effect,” wherein more-diverse communities are more likely to include competitively dominant species that prevent the establishment of new species (Huston 1997, Naeem et al. 2000, Fargione and Tilman 2005).

Although the two mechanisms are not mutually exclusive (Fargione and Tilman 2005), the sampling effect is sometimes regarded as a problematic experimental artifact which creates an apparent, spurious diversity effect (Huston 1997). However, the underlying principle that species differ strongly in their relative resistance to invasion is important in its own right. First, knowing which species are very resistant to invasion even in monoculture would contribute to our understanding of patterns of invasion in habitats containing single-species patches. Secondly, choosing species with strong monoculture resistance would be useful in restoration, because they could limit the subsequent invasion or re-invasion of problem species (D’Antonio and Thomsen 2004). Finally, focusing on single species allows examination of the mechanisms by which individual species should contribute to overall resistance to invasion (Milbau et al. 2003). An understanding of species-specific mechanisms of resistance would be further increased by evaluating how resistance varies with resource additions, and with natural gradients in resource availability, both of which have been shown to exert a controlling effect on the success of added species via their effects on resident competition (Barger et al. 2003, Gerhardt and Collinge 2003, Foster et al. 2004). When resource availability varies across the landscape, understanding the interaction between competitive resistance and environmental conditions can yield predictive insights about the distribution of invasive exotic species (D’Antonio et al. 2001, Dethier and Hacker 2005).

The invasion of exotic annual grasses in many California grasslands is one of the most dramatic examples of the replacement of native vegetation by exotic species. California’s coastal grasslands, however, have been less invaded by Eurasian annual grasses, and now contain a mosaic of native perennial and exotic annual and perennial species (Heady et al. 1977, Hatch et al. 1999). Although in some coastal prairie sites species are very intermingled, in others distinct patches dominated by a single native or exotic species can be readily identified (Peart 1989). Soil characteristics, proximity to coast, latitude, and land use history all influence which native species dominate a given site (Heady et al. 1977, Stromberg and Griffin 1996, Hayes

and Holl 2003). Despite the apparent relative resistance of coastal prairie to exotic annual grasses, several European perennial grass species are increasingly prominent in the habitat, including *Holcus lanatus* (hereafter *Holcus*). *Holcus* is included on the California Invasive Plant Council’s (Cal-IPC) List B: Wildland pest plants of lesser invasiveness (Anderson et al. 1999) and targeted for control by The Nature Conservancy in northern California and the Pacific Northwest (Pitcher and Russo 1988). *Holcus* is a common invader of coastal prairie sites (Elliot and Wehausen 1974, Foin and Hecktner 1986, Peart 1989, Kotanen 2004), although in some sites or patches of prairie, it appears to be relatively limited in its spread (Thomsen et al. 2006, C. D’Antonio, unpubl.).

The extent to which variation in *Holcus*’s abundance across a single site can be attributed to underlying differences in resident plant community composition or to environmental factors is unknown. Competition from resident native perennial grasses is likely to function as an important element of resistance to its invasion, since adult native grasses limit seedling establishment in coastal prairie (Peart 1989, Corbin and D’Antonio 2004). Furthermore, although native coastal prairie grass species have been shown to differ from one another in their competitive interactions with exotic perennial grass species (Thomsen et al. 2006), no information is available as to how established stands of native species differ in their ability to repel exotic perennial grass invaders, or about the mechanisms by which they do so.

Late spring and summer water availability is also likely to influence *Holcus* invasion. Water addition in the late spring and early summer has been shown to increase *Holcus* establishment in a more interior coastal prairie site (Thomsen et al. 2006), and *Holcus* is less common in microhabitats that dry out earlier in the growing season such as hilltops, steep slopes (Thomsen, pers. obs.) and shallow soil patches (Kolb et al. 2002). The ways in which resident species identity and the availability of water and other resources may interact to determine patterns of *Holcus* invasion is unknown.

To examine how three common native coastal prairie species differed from each other and from bare plots in their ability to decrease *Holcus* establishment, we added *Holcus* seed to experimental monocultures and monitored seedling establishment over two growing seasons. We applied a water addition treatment to a subset of these plots, to determine how increased late-season water availability affected resistance, and how the effect of watering varied with resident species identity. To gain insights into the mechanisms by which experimental manipulations altered resistance to *Holcus* invasion, we examined how water and light availability correlated with *Holcus* invasion success. We also examined how native species differed in their effects

on N availability. We then examined the correlation of plant traits with resource levels across species, to gain a more mechanistic understanding of differences among species. The experimental plots were dispersed across a subtle elevational gradient in resource availability and soil texture. We therefore compared *Holcus* seedling establishment within each cover type and watering treatment across this gradient to further evaluate how resource availability interacted with resident species identity in determining invasion resistance.

Methods

Study system

We conducted the experiment at the University of California Bodega Marine Reserve (hereafter, BMR), a coastal prairie about 80 km north of San Francisco in Sonoma County, California (38°18'N, 123°03'W). The grassland areas at BMR occur on sandy soils deriving from Mesozoic granite (Barbour et al. 1973). The BMR climate is typical of coastal northern California, with mean annual temperature of 12°C and mean annual rainfall of 85 cm, 83% of which occurs between November and March (Bodega Marine Laboratory, archived data available at www.bml.ucdavis.edu). Coastal fog modifies the summer–fall drought, significantly decreasing rates of evapotranspiration and thereby delaying the onset of soil moisture deficit (Barbour et al. 1973, Corbin et al. 2005). Much of the BMR grassland has high cover of European annual grass species, although similar to many coastal grassland areas, native perennial grass species are found throughout the site (Kolb et al. 2002). Exotic perennial grasses are also present, and approximately 20% of the BMR grassland is dominated by *Holcus lanatus* (J. Soanes, pers. comm.).

Establishment of cover type and watering treatments

To examine differences among native perennial grass species in their resistance to *Holcus* invasion, we established monoculture plots of three common native grass species: *Bromus carinatus* var. *maritimus*, *Festuca rubra* and *Calamagrostis nutkaensis* (hereafter *Bromus*, *Festuca* and *Calamagrostis*; nomenclature here and elsewhere follows Hickman 1993). We chose these species because they are common and locally dominant in many coastal prairie sites (Hickman 1993). Furthermore, like *Holcus*, they are all perennial bunchgrasses, but they differ in foliage density, phenology, and aboveground biomass. *Bromus* individuals averaged 4 cm in height in experimental plots and have a sparse, sprawling growth form, while *Festuca* and *Calamagrostis*

were on average 30 and 45 cm tall, respectively, and have typical bunchgrass morphologies (below: Hickman 1993). We also established bare plots as controls for native species effects, and *Holcus*-dominated plots to evaluate *Holcus* traits. We refer to the various vegetated plot types and bare plots as 'cover type treatments.'

We collected seeds for *Bromus* and *Calamagrostis* plots in October 1999 at BMR. We collected *Festuca* seeds in July 1998 at Tom's Point, a private nature preserve administered by Audubon Canyon Ranch, 12 km south of BMR (38°13'N, 122°57'W). We cleaned all seeds and germinated them in the greenhouse in November 1999 in 49-ml Fir Cell Containers™ (Stuewe and Sons, Corvallis, OR) filled with sterilized greenhouse soil. We thinned seedlings to one individual per Cone-tainer™ in December 1999. Because *Festuca* seeds were collected off-site, we treated the species as a non-native genotype, in accordance with University of California Natural Reserve System regulations. To prevent it from becoming naturalized at the site, we collected all *Festuca* seeds each year by clipping off the top portion of each flowering culm when seeds were close to mature. We also removed all individuals at the end of the experiment. We also clipped *Calamagrostis* seeds throughout the experiment; we clipped *Bromus* seeds the first year, but time constraints prevented their harvest in subsequent years.

We established the field plots in rows running across a hillside dominated by *Holcus* at BMR; plots were separated by 1.5 m aisles that we mowed each year to minimize *Holcus* seed rain from the surrounding population. In mid-December 1999, we cleared the plots by removing all vegetation with hand tools. We sprayed the edges of all plots and the interiors of all plots except those assigned to the *Holcus* cover treatment with Roundup™ (Monsanto Corporation, St. Louis, MO) in early January 2000 to kill neighboring individuals and emerging seedlings. We raked back vegetation killed by the herbicide application from the plot edges prior to planting.

We assigned cover and watering treatments to plots in a completely randomized design across the slope. There were nine replicates per treatment combination for planted plots and seven for bare plots for the invasion experiment. Due to plant mortality, however, we had to exclude several plots; actual replicate numbers are given in Table 1. We established an additional 20 plots that we left uninvaded and unwatered and planted with *Bromus*, *Festuca*, *Calamagrostis* or *Holcus* (five replicates each) to evaluate species rooting profiles. We also used the uninvaded native plots to evaluate species effects on soil N availability in the absence of *Holcus*.

We planted *Bromus*, *Festuca* and *Calamagrostis* plots between 17 January and 5 February, 2000. We used different densities for the three species, to compensate

Table 1. Replicate numbers for experimental treatments for invaded and uninvaded plots (in parentheses). Uninvaded plots were analyzed separately from the plots used in the invasion experiment.

Cover type	Control	Watered
Bare	7 (0)	7 (0)
<i>Bromus</i>	8 (5)	9 (5)
<i>Festuca</i>	9 (5)	9 (5)
<i>Calamagrostis</i>	8 (5)	9 (5)
<i>Holcus</i>	0 (5)	0 (0)

for differences among them in adult size: 100, 64 and 49 individuals per plot for *Bromus*, *Festuca* and *Calamagrostis*, respectively. We spaced plants evenly within each plot. To create *Holcus* plots, we thinned natural *Holcus* germinants to 64 individuals per plot in May 2000, and weeded out all other germinants. We weeded *Bromus*, *Festuca*, *Calamagrostis* and *Holcus* plots periodically throughout the first growing season to ensure successful seedling establishment, and annually thereafter to maintain monoculture treatments. After *Holcus* seed additions, we no longer weeded *Holcus* seedlings out of invaded plots. We maintained bare plots with twice-yearly herbicide applications until *Holcus* seeds were added; we manually removed forbs and other grass species thereafter.

We hand-watered each plot assigned to the water addition treatment with 7.6 l at weekly intervals twelve times in April through June each year, a total addition of 91 l per plot per year, equivalent to 9.1 cm additional rainfall. We designed this watering treatment to mimic the extended period of high water availability observed during the late spring and early summer in wetter microhabitats or under El Niño weather conditions. Although the amount of added water is small relative to

mean annual rainfall (85 cm; Fig. 1), it represented a 50–260% increase during that time period for the three years of experimental watering, and significantly increased relative soil moisture content during the period of water addition by 7 to 40% (below).

Holcus seed additions and sampling

To invade the experimental plots, we added *Holcus* seeds in November 2001 and 2002. Native plants were well-established at the time of the first seed addition, having completed two growing seasons (Thomsen, pers. obs.). We collected *Holcus* seeds from the surrounding population in August 2001 and 2002. We germinated subsamples of *Holcus* seeds in the lab to assess the number of viable seeds per mg and calculate the mass needed to obtain 2000 seeds m^{-2} , one third of the *Holcus* seed rain measured in native-dominated patches in a heavily invaded coastal prairie site (Peart 1989). We marked a 0.25 m^2 “invasion area” in the center of each plot, to minimize edge effects on *Holcus* seedling performance. In both November 2001 and 2002, we evenly sprinkled 500 seeds inside a frame bordering the invasion area of each plot. In September 2002 and 2003, we sampled the invasion areas using a point frame by examining the area within two cm of 25 evenly spaced points per plot for living *Holcus* seedlings. The September 2002 census samples *Holcus* seedlings that successfully established from a single seed addition (fall 2001) and survived through the first two months of the summer drought period. In September 2003, we sampled the number of *Holcus* seedlings established per plot after two years of seed additions. In both years, we also recorded the total number of *Holcus* inflorescences produced per invasion area.

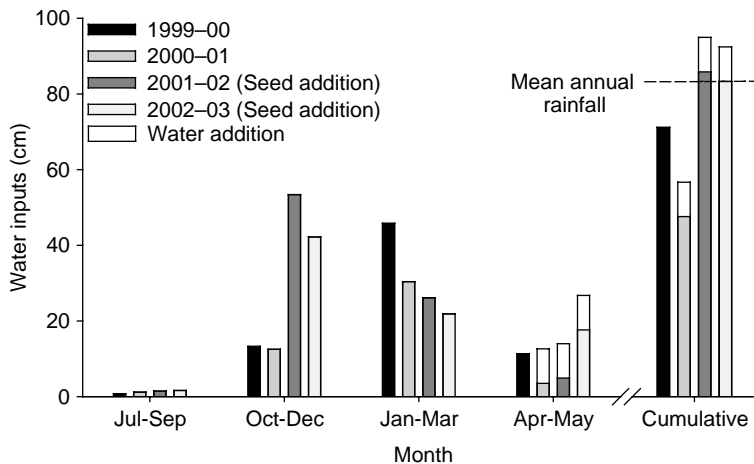


Fig. 1. Quarterly and cumulative water inputs (cm) to experimental plots for each rain year (July–June) of the experiment. The water addition treatment increased total water inputs by 9.1 cm (clear bars) during a relatively dry time of the year (April–June). Dashed line at right indicates mean annual cumulative rainfall (85 cm).

Environmental and plant trait measurements

We surveyed the elevation at the center point of each plot relative to a benchmark using a total station (Topcon Positioning Systems, Inc., Livermore, CA). In August 2003, we collected soil cores (5 cm by 12 cm) immediately outside of 46 randomly-selected plots, stratified by slope position, to evaluate how soil particle size distribution changed across the slope gradient. We dried the samples, separated them into standard particle sizes by five minutes of shaking on a Ro-Tap[®] test sieve shaker (W.S. Tyler, Mentor, OR), and then picked clean of root and other organic material. We weighed the mineral fraction to calculate the percent composition for each particle size class. We used the mass of soil in each core with particle size <2 mm and core area to calculate the mass of non-gravel soil per cm². We then used multiple regression to model grams of soil per cm² as a function of plot elevation and horizontal position. The model only explained 21% of the variation in soil mass/cm², however, so we corrected additional soil measurements (see below) by the overall mean instead of an estimated value based on plot location (mean = 14.1 g soil cm⁻², range = 11.8–17.1 g cm⁻²).

We determined soil percent water content of all plots fourteen times during the experiment using a Moisture Point[®] time domain reflectometry soil moisture sensor with 30 cm probes (E.S.I. Environmental Sensors Inc., Victoria, B.C.; see Thomsen 2005 for sampling dates, minimum, maximum and mean soil moisture values). To generalize soil moisture conditions in each plot throughout the course of the experiment, we standardized soil percent moisture values from each time point as a relative measure by dividing each value by that day's maximum value. We averaged the standardized values from each sampling date to calculate a mean relative soil moisture value for each plot.

We measured the availability of photosynthetically active radiation (PAR) at the soil surface in February 2003 at a single randomly-determined location in each plot using a hand-held quantum sensor (LI-COR Environmental, Lincoln, NE). We measured light availability in all plots within one hour of solar noon on a clear day. This time point provides an intermediate estimate of the light conditions experienced by *Holcus* seedlings during the experiment; it may underestimate light availability for the 2002 seedling census because the resident native plants would have been a bit smaller during the 2001–02 growing season, and overestimate it slightly for the 2003 cohort, because residents would have grown somewhat larger before the seedling census time point. However, multiple measurements seemed unnecessary because resident plant sizes were relatively stable from 2002 to 2003 (Thomsen, unpubl.), and light availability differed strongly across cover types

(below). During the 2002 point-frame censuses, we measured the canopy height at 5 points per plot and averaged the measurements (zero in bare plots).

We used KCl soil extractions to estimate availability of mineral N in uninvaded *Bromus*, *Festuca*, and *Calamagrostis* plots (five plots per cover type), and in five randomly-selected bare plots at distinct time points. We chose these dates to provide insight on N availability at three periods during the growing season: soon after fall wet-up (December 2002), approaching the period of peak biomass (April 2003), and during the summer drought (August 2003). We sampled during the 2002–03 growing season to provide an intermediate estimate of resource availability during the experiment. Just outside the invasion area in each plot we collected two replicate cores (2 cm diameter, 15 cm depth) that we combined and sieved through 2 mm mesh. We dried a weighed subsample at 100C and re-weighed it to determine gravimetric water content. We added 50 ml 2M KCl to a 13 g sample of wet soil (10–12 g dry) and placed the slurry on an orbital shaker for 45 min. We filtered the extracts on pre-leached Whatman 40 Quantitative Grade Filter Paper (Whatman Group, Middlesex, U.K.) and froze them until analyzing them for ammonium and nitrate concentration on a Lachat Autoanalyzer (Lachat Instruments, Loveland, CO). We corrected ion concentrations for molecular weight of N, gravimetric water content and grams of non-gravel soil per cm² to calculate µg available N per cm² of soil.

We sampled root biomass in the five uninvaded, unwatered *Bromus*, *Festuca*, *Calamagrostis* and *Holcus* plots in July 2003. We collected five incremental cores of 12 cm depth per plot (total depth in each plot = 60 cm) and kept them refrigerated until processing. We washed each core clean of mineral soil using a soil elutriator (Bel-Art Products, Pequannock, NJ), and collected all roots and other organic material on a 500 µm sieve. We re-suspended this material in still water and picked out all non-root material, collected the cleaned roots (living and dead) on a sieve and dried and weighed them.

Data analysis

We analyzed our data using JMP IN[®] 3.2.6 (SAS Institute Inc., Cary, NC). Because of the differences in sampling each year, (i.e. the initial sampling represents *Holcus* success the first year of seed addition and the second an overall invasion success over two years), we analyzed the data from the two years of *Holcus* seed additions separately. *Holcus* seedling numbers, canopy height, mean relative water availability and soil N estimates met assumptions of normality and equality of variances without transformation. We used square-root

transformations for *Holcus* flowering culm data, and log-transformed light and root biomass measurements.

We evaluated cover type and watering treatment effects on *Holcus* seedling numbers and the number of flowering culms per plot using two-way anova. We used post-hoc Tukey means' comparisons to assess pairwise differences among groups for all significant factors (Zar 1999); in several cases, we used t-tests to examine the effect of watering within plots of a single cover type. We used regressions to evaluate the relationship of relative water availability and light levels with the number of *Holcus* seedlings and flowering culms, across cover type and watering treatments. We examined the effect of cover type on N availability in the uninvaded plots with one-way anova. We tested the differences among the three native species and *Holcus* in their rooting profiles using repeated measures anova with species as the fixed factor and depth increment as the repeated variable. To evaluate the relationships among cover types, plant traits and environmental factors we used one-way anova.

We used regressions to characterize the effect of plot elevation on soil texture and relative water availability. To evaluate the interaction of elevation with cover and watering treatments, we used regressions to test the relationship between elevation and the number of *Holcus* seedlings and flowering culms for each year in each cover and watering treatment combination. Because these are *a priori* planned independent comparisons, we used $p < 0.05$ to determine the significance of these relationships. We used regression to test the effect of elevation and watering treatment on resident species canopy height.

Results

Effects of cover type and watering treatment

Cover type had a significant effect on the number of living *Holcus* seedlings sampled per invasion area in September 2002 (Table 2): there were almost twice as many *Holcus* seedlings in bare and *Bromus* plots as in plots dominated by *Festuca* and *Calamagrostis* (Fig. 2a). The main effect of watering was not significant, but

there was a trend towards a significant interaction of cover type and watering treatment in their effects on *Holcus* seedling numbers in 2002 ($p = 0.065$). Within *Bromus* plots there were 67% more *Holcus* seedlings sampled per plot in watered than ambient rainfall plots ($t_{15} = 2.41$; $p = 0.029$) but seedling numbers did not respond to watering treatment within any other cover type ($p > 0.2$). Cover types also differed in the number of *Holcus* flowering culms. *Bromus* plots had the greatest mean number of culms (58.6), bare plots were intermediate (14.5), and *Festuca* and *Calamagrostis* plots had an average of 1.5 culms (Fig. 2b). The number of *Holcus* flowering culms was not affected by watering treatment. The number of culms was marginally affected by an interaction between cover type and watering treatment ($p = 0.067$), with a non-significant trend for greater numbers of *Holcus* culms in watered *Bromus* plots, ($t_{15} = 1.85$; $p = 0.084$).

The September 2003 census shows a similarly strong effect of cover type on the number of living *Holcus* seedlings sampled (Table 2). Bare and *Bromus* plots had more than five times as many living *Holcus* seedlings as *Festuca* and *Calamagrostis* plots (Fig. 2c). Neither watering nor the interaction of cover and watering treatments had a significant effect on the number of *Holcus* seedlings sampled. The number of *Holcus* flowering culms per invasion area at this time point was significantly affected by cover type but not by watering treatment or the interaction of the two variables (Table 2). Bare and *Bromus* plots had an average of 56 *Holcus* culms per invasion area, while *Festuca* and *Calamagrostis* plots had three (Fig. 2d).

Resource availability and species traits

Regressions showed that mean water availability was not correlated with *Holcus* seedling or flowering culm numbers across all plots in either year ($R^2 < 0.01$; $F_{1,65} < 0.73$; $p > 0.3$), and one-way anova indicated that it did not differ significantly with cover type (Table 3). In contrast, light availability was strongly correlated with *Holcus* seedling and flowering culm numbers across cover and watering treatments in both

Table 2. Results of two-way anovas testing the effect of experimental manipulations on the number of *Holcus* seedlings and flowering culms per invasion area in fall 2002 and 2003. Cover = cover type and +H₂O = watering treatment. Data were analyzed separately for each variable each year.

Treatment	DF	Alive 2002		Culms 2002		Alive 2003		Culms 2003	
		F	p	F	p	F	p	F	p
Cover	3,59	17.00	0.0001	40.50	0.0001	83.86	0.0001	136.9	0.0001
+H ₂ O	1,59	1.59	0.212	1.52	0.222	0.85	0.359	0.29	0.589
Interaction	3,59	2.54	0.065	2.51	0.067	1.69	0.178	1.53	0.216

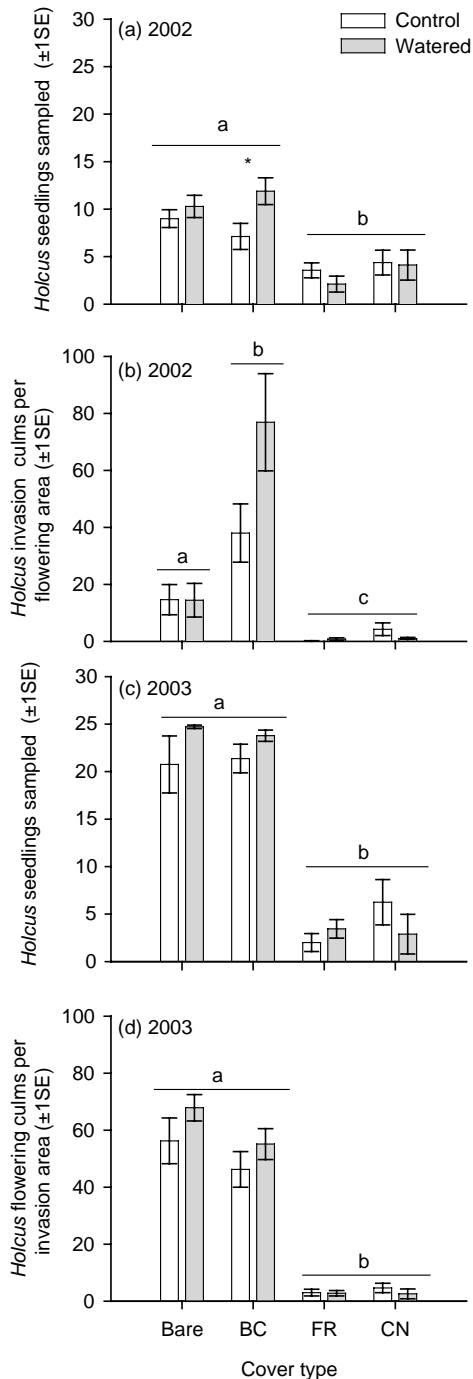


Fig. 2. Mean number of *Holcus* seedlings sampled and *Holcus* flowering culms per invasion area, ± 1 SE, for the two years of sampling. BC = *Bromus*, FR = *Festuca*, and CN = *Calamagrostis* cover types; clear bars represent control and gray bars watered treatment plots. See Table 2 for anova statistics. Letters represent cover type treatments that are significantly different in Tukey post-hoc means' comparisons. The asterisk marks the significant effect of water addition within *Bromus* plots on *Holcus* seedling numbers in 2002.

years of the experiment (Table 4). Cover types differed significantly in light availability (Table 3), with bare plots having the highest availability of photosynthetically active radiation (irradiance = $621 \mu\text{mol m}^{-2} \text{s}^{-1}$), *Bromus* plots intermediate levels ($361 \mu\text{mol m}^{-2} \text{s}^{-1}$), and *Festuca* and *Calamagrostis* plots having similarly low light levels ($18 \mu\text{mol m}^{-2} \text{s}^{-1}$; Fig. 3a). Canopy height followed the reverse pattern across cover type ($F_{3,63} = 175.89$, $p < 0.0001$), with bare and *Bromus* plots having similarly short canopies (zero and 3.5 cm, respectively), *Festuca* plots intermediately tall canopies (29.1 cm), and *Calamagrostis* plots the tallest (46.1 cm; Fig. 3b). Canopy height had a significant negative relationship with light level across all plot types ($R^2 = 0.69$, $F_{1,65} = 142.05$, $p < 0.0001$; Fig. 3c).

Cover types differed significantly in N availability in December 2002 and August 2003 (Table 3), but not in April 2003 (Fig. 4a-c). Tukey tests indicate that in December 2002, soon after the first fall rains, bare plots had more than twice as much available N as *Festuca* and *Bromus* plots; *Calamagrostis* plot N levels were intermediate between the other cover types. In August 2003, in the middle of the summer drought period, *Festuca* plots had approximately half the amount of available N of *Bromus* plots, while bare and *Calamagrostis* plot N availability was intermediate.

Root biomass (measured in August 2003) differed significantly among species throughout the 60 cm depth profile ($F_{12,32} = 13.82$, $p < 0.0001$; Fig. 5a). *Festuca* plots had more than twice the root biomass of *Bromus*, *Calamagrostis* and *Holcus* plots in the surface increment (0–12 cm); in the 12–48 cm depth increments, *Festuca* and *Calamagrostis* had approximately twice the root biomass of *Holcus* and *Bromus*. There was a significant negative linear relationship between the mean shallow root biomass (0–12 cm depth) of the three native species and August N availability ($R^2 = 0.41$, $F_{1,13} = 9.032$, $p = 0.01$; Fig. 5b).

Table 3. Results of one-way anovas testing the effect of cover type on mean water availability, light and nitrogen availability in experimental plots. Water and light were measured in invaded plots and nitrogen availability was measured in uninvaded plots.

Resource	DF	F	p
Water	3,63	1.46	0.235
Light	3,63	46.60	<0.0001
December N	3,16	8.04	0.002
April N	3,16	1.77	0.193
August N	3,16	5.01	0.012

Table 4. Regression parameters for the relationship between *Holcus* seedling or flowering culm numbers and light availability across all experimental plots, and for cover type and watering treatment combinations for which there was a significant relationship ($p < 0.05$) between *Holcus* seedling or flowering culm numbers and plot elevation. CN = *Calamagrostis*, BC = *Bromus*, and +H₂O = watering treatment. The final column indicates whether the relationship between the two variables was positive or negative.

Variable	Treatment	DF	F	p	R ²	+/-
Effect of light on seedling and culm numbers across treatments						
Seedlings 2002		1,65	34.30	<0.0001	0.35	+
Seedlings 2003		1,65	60.97	<0.0001	0.48	+
Culms 2002		1,64	7.44	0.008	0.10	+
Culms 2003		1,65	85.49	<0.0001	0.57	+
Effect of elevation on seedling and culm numbers						
Seedlings 2002	CN +H ₂ O	1,7	14.77	0.007	0.68	+
Seedlings 2003	CN +H ₂ O	1,7	5.80	0.047	0.45	+
Culms 2002	Bare +H ₂ O	1,5	7.11	0.045	0.59	-
Culms 2002	BC control	1,6	10.80	0.017	0.64	-
Culms 2002	BC +H ₂ O	1,7	8.01	0.025	0.53	-

Resistance and plot elevation

The total change in elevation from the bottom to the top of the experimental array was 4.6 m, corresponding to an average slope of 15%. Although the mass of soil per core with particle diameter <2 mm did not differ significantly with plot elevation (see above), the mass in the >2 mm size class increased significantly with elevation from approximately 20 g per core at the bottom of the slope to 60 g per core at the top ($R^2 = 0.31$; $F_{1,44} = 19.9$, $p < 0.0001$; Fig. 6a). Five of the fourteen soil moisture sampling dates showed a significant decrease in relative water availability towards the top of the slope, with the percentage decrease ranging from 33% to 57% ($R^2 = 0.20-0.30$; $F_{1,65} = 9.5-26.1$; $p < 0.004$). The average of those five dates' mean relative water availability is shown as a function of elevation in Fig. 6b ($R^2 = 0.43$, $F_{1,65} = 49.64$; $p < 0.0001$).

When the relationship between elevation and the number of *Holcus* seedlings sampled or flowering culms per invasion area was evaluated separately for every cover and watering treatment combination for both years, four had a slope significantly different from zero at $p < 0.05$ (Table 4). The number of *Holcus* flowering culms per invasion area decreased from 45 at the bottom of the slope to 5 at the top in bare watered plots, and from 140 to 20 and 78 to 6 in control and watered *Bromus* plots, respectively, in 2002 (Fig. 7a–b). The significance of the relationship for bare watered plots disappears, however, if the single low-elevation plot is removed from the analysis. In watered *Calamagrostis* plots the number of living *Holcus* seedlings sampled per invasion area increased from zero at the bottom to 12 at the top of the slope in 2002 (Fig. 7c). None of the regressions for *Festuca* plots or for 2003 seedling or culm numbers were significant.

To evaluate the possibility that *Holcus* seedling numbers and flowering culm production were responding to changes in resident plant performance across the slope, *Bromus* and *Calamagrostis* canopy heights were examined as a function of elevation. *Bromus* canopy height in 2002 decreased by 70% from the bottom to the top of the slope in watered plots ($R^2 = 0.60$, $F_{1,7} = 10.60$, $p = 0.014$; Fig. 8a), but there was no significant relationship between *Bromus* canopy height and elevation in control plots ($R^2 = 0.001$, $F_{1,6} = 0.004$, $p = 0.949$). *Calamagrostis* canopy height in 2002 also had a significant negative relationship with elevation in watered plots ($R^2 = 0.65$, $F_{1,7} = 12.88$, $p = 0.009$), decreasing by approximately 50% from the bottom to the top (Fig. 8b). In control plots, elevation was not correlated with *Calamagrostis* canopy height ($R^2 = 0.06$, $F_{1,6} = 0.35$, $p = 0.576$).

Discussion

How do California native grass species differ in their resistance to *Holcus* invasion?

Many researchers have suggested that the greater invasion resistance of diverse communities is due in part to a sampling effect, whereby high species richness increases the likelihood of the presence of strong competitors that are highly resistant even in monoculture (Huston 1997, Naeem et al. 2000, Fargione and Tilman 2005). This explanation is based on the premise that individual species differ in their resistance to invasion, an idea supported by the results reported here. We found that monocultures of two native California bunchgrasses, *Festuca rubra* and *Calamagrostis nutkaenesis*, were very resistant to invasion by the widespread European perennial grass *Holcus lanatus*, as measured by both the number of

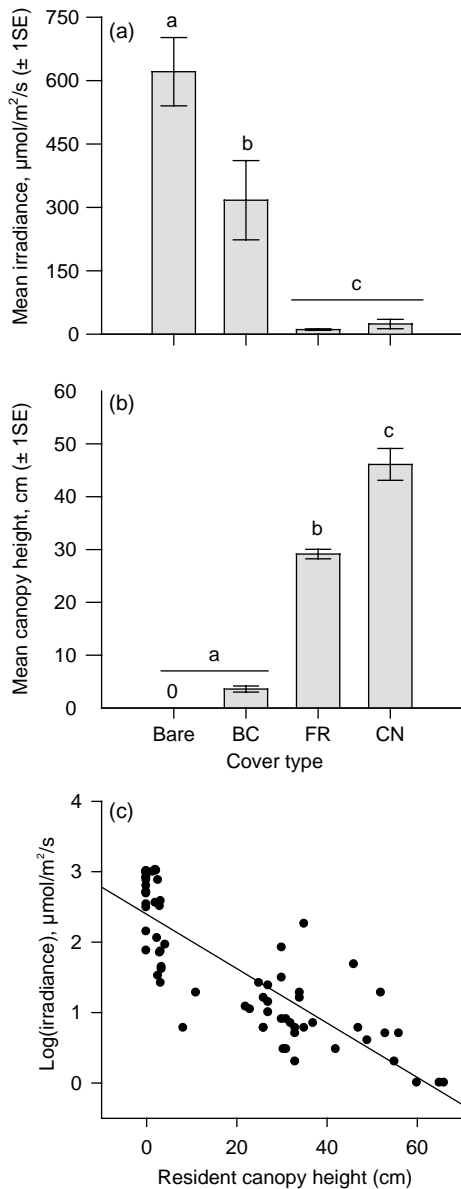


Fig. 3. Relationships between light availability at the soil surface, canopy height, and plot cover type. BC = *Bromus*, FR = *Festuca*, and CN = *Calamagrostis* cover types. See Table 3 and text for anova and regression statistics. Letters indicate cover type treatments that have significantly different light availability or canopy height in Tukey post-hoc means' comparisons.

Holcus seedlings and flowering culms produced per plot. In contrast, plots of a third common California native grass, *Bromus carinatus* var. *maritimus*, were invaded by *Holcus* at a level at least equivalent to that of bare plots. In fact, in the first year of seed addition, *Holcus* flowering culm production was greater in *Bromus* plots than in bare plots. *Bromus* individuals

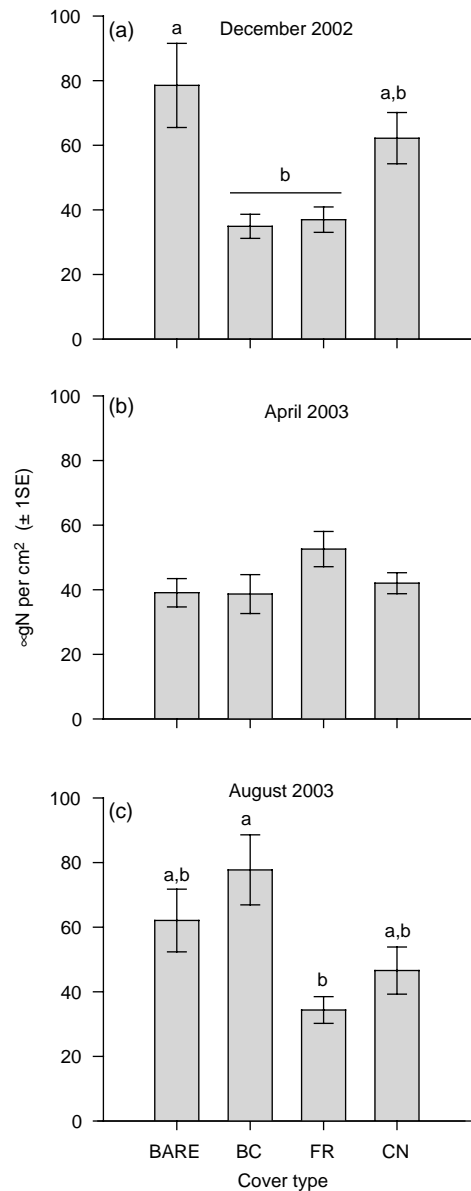


Fig. 4. N availability in unininvaded plots at three time points during the 2002–03 growing season. BC = *Bromus*, FR = *Festuca*, and CN = *Calamagrostis* cover types. See Table 3 for anova statistics. Letters indicate cover type treatments that have significantly different N availability in Tukey post-hoc means' comparisons.

may have provided some protection from the wind and sun for *Holcus* seedlings (Thomsen, pers. obs.). If so, this pattern supports the idea that resident community members could facilitate the establishment of invasive species when abiotic conditions are harsh (Bruno et al. 2003).

Variation among the three native species in their effect on light availability appears to explain much of

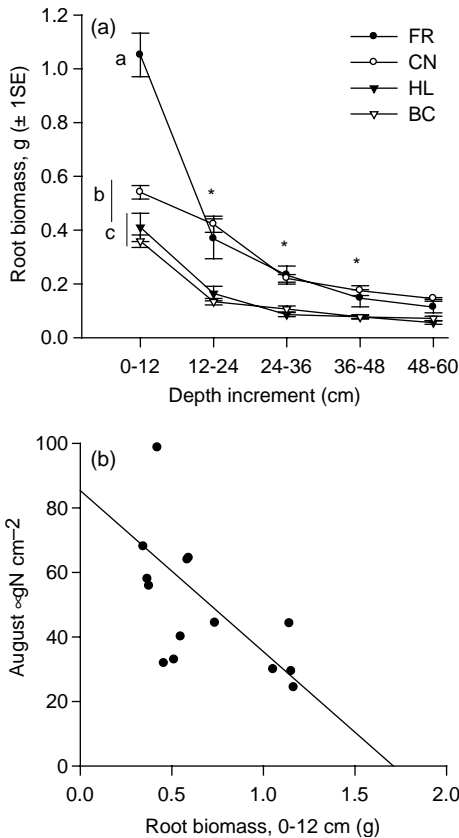


Fig. 5. Root biomass in August 2003 through 60 cm of depth across cover types, and the relationship between shallow (0–12 cm) root biomass and August 2003 N availability in uninvaded plots (*Bromus*, *Festuca* and *Calamagrostis* plots only). BC = *Bromus*, FR = *Festuca*, CN = *Calamagrostis*, and HL = *Holcus* cover types. See text for anova and regression statistics. Letters indicate cover type treatments that have significantly different root biomass in the 0–12 cm increment and stars mark significant differences between the root biomass of the species pairs *Festuca/Calamagrostis* and *Bromus/Holcus* (Tukey tests).

their relative resistance to *Holcus* invasion. Lower light availability was associated with lower numbers of *Holcus* seedlings and flowering culms across all plot types, and *Festuca* and *Calamagrostis*, the least-invaded native species, decreased light availability to a much greater extent than *Bromus*. This is likely due to the significantly greater canopy height of *Festuca* and *Calamagrostis*, which correlated with light availability across plot types. Low light availability has been shown to limit seedling establishment in other perennial grass-dominated systems (Peart 1989, Naeem et al. 2000, Foster et al. 2002, Milbau et al. 2005), and low likelihood of weed invasion in perennial grassland restoration sites has been linked to decreased light availability (Blumenthal et al. 2005).

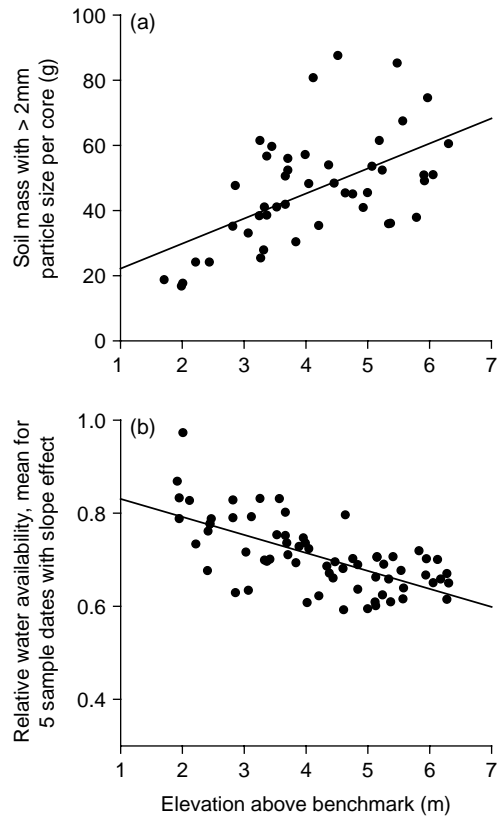


Fig. 6. Effect of plot elevation on soil texture and mean relative water availability. In (b), the average value for each plot is shown for the five soil moisture sample dates that on which there was a significant relationship between plot relative water availability and elevation. See text for regression statistics.

Thus, the establishment or maintenance of dense stands of native grasses could be critical to the management of invasion resistance in perennial grasslands (Milbau et al. 2005). Restoration projects that include relatively tall native species like *Festuca* and *Calamagrostis* may successfully decrease light availability at the soil surface and thus decrease the chances of invasive plant establishment.

Species effects on soil N may also have contributed to patterns of relative resistance in this experiment. Although the relationship between N availability and *Holcus* seedling and culm numbers cannot be directly investigated, one of the strongly resistant native species, *Festuca rubra*, had lower levels of available soil N than bare plots in December and than *Bromus* plots in August. *Festuca*'s high shallow root biomass may allow it to deplete N availability near the surface more effectively than other species studied, since shallow root biomass was significantly negatively correlated with August N availability across cover types. Alternatively, high root biomass in *Festuca* plots may promote high microbial

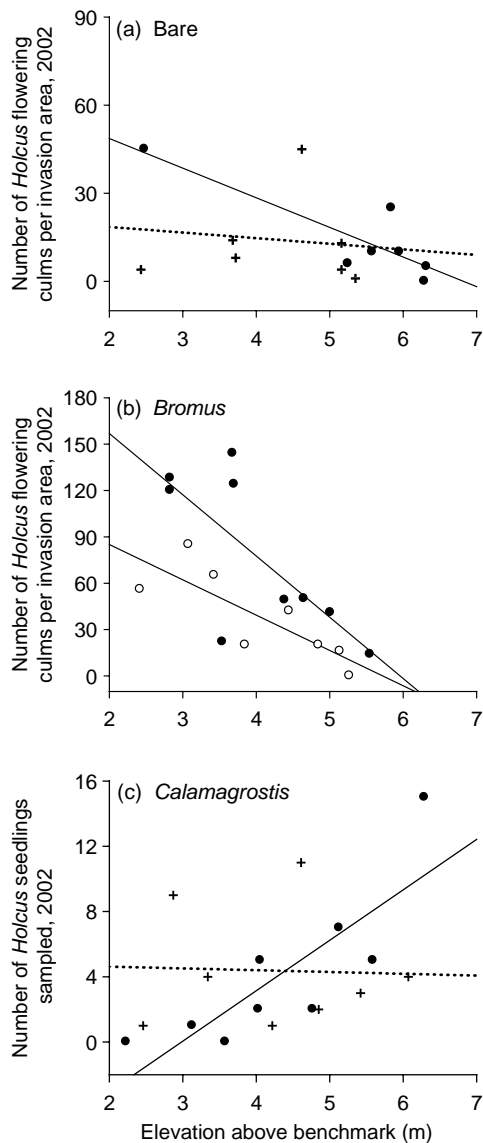


Fig. 7. Relationships between plot elevation and *Holcus* flowering culm and seedling numbers in watered and control bare, *Bromus* and *Calamagrostis* plots. For significant regressions, ○ = control and ● = watered plots; + = control plots for non-significant regressions. See Table 4 for regression statistics.

immobilization of soil N. With either mechanism, *Festuca* plots would have lower N availability for *Holcus* seedlings. Highly-invaded *Bromus* plots, however, also had low N availability in December, and the strongly resistant *Calamagrostis* plots had intermediate N levels at both time points. Thus, N availability does not appear to play a strong role in the relative resistance to invasion of these native species.

The lack of a controlling effect of soil N on patterns of invasion in this study differentiates it from

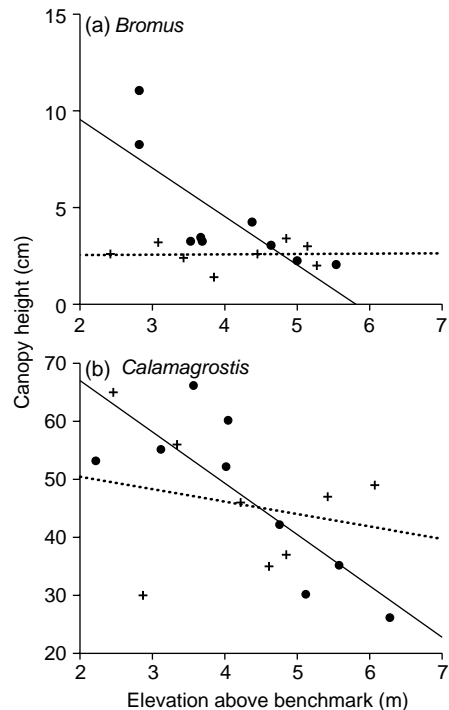


Fig. 8. *Bromus* and *Calamagrostis* canopy heights as a function of plot elevation. For significant regressions, ● = watered plots; + = control plots for non-significant regressions. See text for regression statistics.

several studies in which nutrient availability has been shown to be a key element in determining grassland invasibility (Kolb et al. 2002, Prieur-Richard et al. 2002, Barger et al. 2003, Fargione and Tilman 2005). Because of a research focus on the effects of soil N, the role of light limitation in determining grassland invasibility may have received less attention than it deserves. One possible consequence of this oversight is that management strategies intended to reduce standing biomass and thus mitigate the effects of anthropogenic increases in N, such as grazing (Weiss 1999), mowing (Maron and Jeffries 2001) or fire may be adopted without considering their effects on the canopy closure of well-established native grass stands. In the absence of specific information indicating a relative benefit to native species, the possibility that these activities could ultimately facilitate invasion should be considered.

The role of water availability and landscape heterogeneity in *Holcus* invasion

Several lines of evidence suggest that water availability during the spring and summer months could influence *Holcus*'s ability to invade in California prairie sites. Its

distribution appears to follow patterns of soil moisture availability at the landscape level (Thomsen, pers. obs.; Kolb et al. 2002), and adding water from April to June increased the number, survival, and inflorescence production of *Holcus* seedlings in a more interior coastal prairie site (Thomsen et al. 2006). Here, a watering treatment applied during the same time period resulted in significantly more *Holcus* seedlings in *Bromus* plots in 2002, the drier of the two invasion years, but had no overall effect on *Holcus* seedling numbers or flowering culm production across cover treatments. Furthermore, mean relative water availability was not significantly correlated with *Holcus* seedling or culm numbers. The watering treatment had no effect despite the fact that it significantly increased soil moisture and represented a substantial increase over ambient water inputs during the treatment period (Fig. 1).

Although the watering treatment had little effect on *Holcus* invasion, cover type interacted with the elevational gradient in ways that suggested that abiotic conditions, including water availability, do influence *Holcus* performance at BMR. *Holcus* culm numbers decreased towards the top of the slope in bare and *Bromus* plots, probably in response to greater abiotic stress associated with coarser soil texture and lower water availability at the top of the slope. Increased competition is unlikely to drive this pattern since *Holcus* seedlings were free from competition in bare plots and *Bromus* canopy height either responded negatively (watered plots) or not at all (controls) to higher elevation. In contrast, 2002 *Holcus* seedling numbers increased at higher elevation in *Calamagrostis* plots as *Calamagrostis* canopy height decreased, indicating that the strong resistance by *Calamagrostis* low on the slope was weakened where abiotic conditions were worse (higher on the slope). The lowered competitive resistance of *Calamagrostis* at the top of the slope may reflect its sensitivity to water availability, since its phenology extends later into the summer drought period and it shows greater dependence on fog-derived water in the late summer than other California native grasses (Corbin et al. 2005).

The opposing effects of elevation in *Calamagrostis* and *Bromus* plots represents an interaction between biotic and abiotic forms of resistance: the effect of slope position depends on resident identity. Interactions between biotic and abiotic resistance have the potential to provide mechanistic explanations for patterns of invasion (D'Antonio et al. 2001, Gerhardt and Collinge 2003, Dethier and Hacker 2005). For example, species interactions can vary from competitive to facultative across environmental gradients, suggesting that residents providing competitive resistance under some conditions might actually facilitate invader establishment in others (Simberloff and Von Holle 1999, Bruno et al. 2003). Thus, it cannot be assumed that an invasive

species will respond to environmental conditions the same way everywhere it becomes established; instead, its response will also be a function of resident community composition (D'Antonio et al. 2001). Furthermore, understanding how an invasive species responds to physical conditions under different community contexts can provide valuable insights about how best to manage invaded ecosystems (D'Antonio and Thomsen 2004, Dethier and Hacker 2005). Here, the decrease in resistance to *Holcus* invasion towards the bottom of the slope in bare and *Bromus* plots, apparently due to the better abiotic conditions found there, suggests that where resident community resistance is low, favorable sites such as swales may be highly vulnerable to invasion. In contrast, when the resident community provides strong biotic resistance, as in *Calamagrostis* patches, areas with beneficial conditions may be relatively protected by residents, and management could focus on the removal of invasive individuals in upslope areas.

Further implications

The strong resistance of *Festuca* and *Calamagrostis* plots observed in this study suggests that if dense stands of some native species can be established or maintained in California coastal prairie sites, they may be able to resist *Holcus* invasion. *Holcus* has, however, been observed to enter grassland areas dominated by *Festuca rubra* and similar bunchgrasses (D'Antonio, pers. obs.). Since the resistance of *Festuca* and *Calamagrostis* plots was not complete, it is possible that even the low numbers of surviving *Holcus* seedlings seen in *Festuca* and *Calamagrostis* plots may be enough to allow the gradual establishment of a *Holcus* population over many years. Since natural stands are likely to be more spatially or temporally variable than the experimental ones used here, they are also likely to be more invasible (Davis and Pelsor 2001). *Holcus* could primarily enter patches dominated by exotic annuals or less-competitive native species, or invade small soil disturbances in which the competitive effects of resident species are disrupted (Thomsen 2005).

Holcus's presence in native-dominated coastal prairie sites may also be related to the cessation of livestock grazing, which is associated with increasing dominance by both native and exotic perennial grass species at the expense of exotic annuals in coastal prairie (Elliot and Wehausen 1974, Foin and Heckner 1986). Annuals may increase under grazed conditions because of their greater ability to set seed despite springtime grazing, their ability to colonize new open spaces, and tolerance of low-mulch conditions (Elliot and Wehausen 1974). Under this scenario, perennial species increase in cover

when grazers are removed (although see Hatch et al. 1999 and Hayes and Holl 2003).

Vegetation history at BMR fits the model of increasing native and exotic perennial dominance with recovery from grazing. Eleven years after the removal of grazing animals, the BMR grasslands were dominated by exotic annual grass and forb species (Barbour et al. 1973). The two most common native perennial grasses (*Poa secunda* and *Bromus carinatus*) had an estimated 2% cover, and *Holcus* was uncommon outside of seasonally wet areas (Barbour et al. 1973). In contrast, forty years after livestock removal, Kolb et al. (2002) documented much higher cover of perennial grasses: the two most common native perennial grasses, *Hordeum brachyantherum* and *B. carinatus* together had 5–18% cover across several types of grassland areas. *Holcus* cover ranged from 1–5%, but the areas sampled in the study are outside the main area of *Holcus* invasion (Kolb et al. 2002); Reserve-wide, *Holcus* is now estimated to dominate 20% of the grassland area (J. Soanes, pers. comm.).

The fact that native and exotic perennial grasses may respond similarly to long-term land use changes (in this case release from grazing) in California coastal prairie is an example of the conundrum facing the managers of ecosystems in which desirable native species and problematic invasive species respond similarly to management activities (Kotani 1997, McGraw 2004). The cessation of grazing does appear to result in a net gain in native species dominance, since native and exotic perennial grasses are replacing exotic annual species (Elliot and Wehausen 1974, Foin and Heckner 1986). It remains to be seen, however, if native species can ultimately hold their own in the face of increasing competition from exotic perennial grass species (Kotani 2004).

Acknowledgements – This work was supported by a National Science Foundation Graduate Research Fellowship, a Univ. of California Natural Reserve System Mildred E. Matthias Student Research Grant, an East Bay Chapter of the California Native Plant Society Scholarship, and a Marshall and Nellie Alworth Memorial Fund Scholarship. Thanks to Peter Connors and Rico Tinsman at the Bodega Marine Reserve for technical advice and logistical assistance. This is contribution no. 2349, Bodega Marine Laboratory, Univ. of California at Davis.

References

- Alpert, P., Bone, E. and Holzapfel, C. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. – *Persp. Plant Ecol. Evol. Syst.* 3: 52–66.
- Anderson, L., DiTomaso, J., Hrusa, G. F. et al. 1999. The CalEPPC list: exotic pest plants of greatest ecological concern in California. – CA Inv. Plant Council.
- Barbour, M. G., Craig, R. B., Drysdale, F. R. et al. 1973. Coastal ecology: Bodega Head. – Univ. California Press.
- Barger, N. N., D'Antonio, C. M., Thaura, G. et al. 2003. Constraints to colonization and growth of the African grass, *Melinis minutiflora*, in a Venezuelan savanna. – *Plant Ecol.* 167: 31–43.
- Blumenthal, D. M., Jordan, N. R. and Svenson, E. L. 2005. Effects of prairie restorations on weed invasions. – *Agric. Ecosystem Environ.* 107: 221–230.
- Bruno, J. F., Stachowicz, J. J. and Bertness, M. D. 2003. Inclusion of facilitation into ecological theory. – *Trends Ecol. Evol.* 18: 119–125.
- Corbin, J. D. and D'Antonio, C. M. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. – *Ecology* 85: 1273–1283.
- Corbin, J. D., Thomsen, M. A., Dawson, T. E. et al. 2005. Summer water use by California coastal prairie grasses: fog, drought, and community composition. – *Oecologia* 145: 511–521.
- D'Antonio, C., Levine, J. and Thomsen, M. 2001. Ecosystem resistance to invasion and the role of propagule supply: a California perspective. – *J. Med. Ecosystems* 2: 233–246.
- D'Antonio, C. M. and Thomsen, M. 2004. Ecological resistance in theory and practice. – *Weed Tech.* 18: 1572–1577.
- Davies, K. F., Chesson, P., Harrison, S. et al. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. – *Ecology* 86: 1602–1610.
- Davis, M. A. and Pelsor, M. 2001. Experimental support for a resource-based mechanistic model of invasibility. – *Ecol. Lett.* 4: 421–428.
- Dethier, M. N. and Hacker, S. D. 2005. Physical factors vs. biotic resistance in controlling the invasion of an estuarine marsh grass. – *Ecol. Appl.* 15: 1273–1283.
- Elliot, H. W. and Wehausen, J. D. 1974. Vegetational succession on coastal rangeland of Point Reyes Peninsula. – *Madroño* 22: 231–238.
- Elton, C. S. 1958. The ecology of invasions by animals and plants. – Methuen & Co.
- Fargione, J. E. and Tilman, D. 2005. Diversity decreases invasion via both sampling and complementary effects. – *Ecol. Lett.* 8: 604–611.
- Foin, T. C. and Heckner, M. M. 1986. Secondary succession and the fate of native species in a California coastal prairie community. – *Madroño* 33: 189–206.
- Foster, B. L., Smith, V. H., Dickson, T. L. et al. 2002. Invasibility and compositional stability in a grassland community: relationships to diversity and extrinsic factors. – *Oikos* 99: 300–307.
- Foster, B. L., Dickson, T. L., Murphy, C. A. et al. 2004. Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. – *J. Ecol.* 92: 435–449.
- Gerhardt, F. and Collinge, S. K. 2003. Exotic plant invasions of vernal pools in the Central Valley of California, USA. – *J. Biogeogr.* 30: 1043–1052.
- Hatch, D. A., Bartolome, J. W., Fehmi, J. S. et al. 1999. Effects of burning and grazing on a coastal California grassland. – *Restor. Ecol.* 7: 376–381.

- Hayes, G. F. and Holl, K. D. 2003. Cattle grazing on annual forbs and vegetation composition of mesic grasslands in California. – *Conserv. Biol.* 17: 1694–1702.
- Heady, H. F., Foin, T. C., Hektner, M. M. et al. 1977. Coastal prairie and northern coastal scrub. – In: Barbour, M. G. and Major, J. (eds), *Terrestrial vegetation of California*. Wiley-Interscience, pp. 733–760.
- Hickman, J. C. (ed.) 1993. *The Jepson manual: higher plants of California*. – Univ. California Press.
- Hooper, D. U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. – *Ecology* 79: 704–719.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. – *Oecologia* 110: 449–460.
- Kolb, A., Alpert, P., Enters, D. et al. 2002. Patterns of invasion within a grassland community. – *J. Ecol.* 90: 871–881.
- Kotanen, P. M. 1997. Effects of experimental soil disturbance on revegetation by natives and exotics in coastal Californian meadows. – *J. Appl. Ecol.* 34: 631–644.
- Kotanen, P. M. 2004. Revegetation following soil disturbance and invasion in a Californian meadow: a 10-year history of recovery. – *Biol. Invasions* 6: 245–254.
- Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. – *Science* 288: 852–854.
- Levine, J. M., Vila, M., D'Antonio, C. M. et al. 2003. Mechanisms underlying the impacts of exotic plant invasions. – *Proc. R. Soc. Lond. B* 270: 775–781.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. – *Ecology* 80: 1522–1536.
- Mack, R. N., Simberloff, D., Lonsdale, M. W. et al. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. – *Ecol. Appl.* 10: 689–710.
- Maron, J. L. and Jefferies, R. L. 2001. Restoring enriched grasslands: effects of mowing on species richness, productivity, and nitrogen retention. – *Ecol. Appl.* 11: 1088–1100.
- Milbau, A., Nijs, I., Van Peer, L. et al. 2003. Disentangling invasiveness and invasibility during invasion in synthesized grassland communities. – *New Phytol.* 159: 657–667.
- Milbau, A., Nijs, I., de Raedemaeker, F. et al. 2005. Invasion in grassland gaps: the role of neighborhood richness, light availability and species complementarity during two successive years. – *Funct. Ecol.* 19: 27–37.
- McGraw, J. M. 2004. Interactive effects of disturbance and exotic species on the structure and dynamics of an endemic sandhills plant community. – PhD. thesis, Univ. California, Berkeley.
- Naeem, S., Knops, J. M. H., Tilman, D. et al. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. – *Oikos* 91: 97–108.
- Peart, D. R. 1989. Species interactions in a successional grassland. III. Effects of canopy gaps, gopher mounds, and grazing on colonization. – *J. Ecol.* 77: 267–289.
- Pitcher, D. and Russo, M. J. 1988. Element stewardship abstract for *Holcus lanatus*. – The Nature Conservancy.
- Prieur-Richard, A.-H., Lavorel, S., Dos Santos, A. et al. 2002. Mechanisms of resistance of Mediterranean annual communities to invasion by *Coryza bonariensis*: effects of native functional composition. – *Oikos* 99: 338–346.
- Rejmanek, M. 1996. Species richness and resistance to invasion. – In: Orians, G. H., Dirzo, R. and Cushman, J. H. (eds), *Diversity and process in tropical forest ecosystems*. Springer-Verlag, pp. 153–172.
- Simberloff, D. and Von Holle, B. 1999. Positive interactions of nonindigenous species: invasional meltdown? – *Biol. Invasions* 1: 21–32.
- Stohlgren, T. J., Binkley, D., Chong, G. W. et al. 1999. Exotic plant species invade hot spots of native plant diversity. – *Ecol. Monogr.* 69: 25–46.
- Stromberg, M. R. and Griffin, J. R. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. – *Ecol. Appl.* 6: 1189–1211.
- Thomsen, M. A. 2005. Ecological resistance, propagule supply and the invasion of California coastal prairie by the European grass *Holcus lanatus* L. – PhD. thesis, Univ. California, Berkeley.
- Thomsen, M. A., D'Antonio, C. M., Suttle, K. B. et al. 2006. Ecological resistance, seed density, and their interactions determine patterns of invasion in a California coastal grassland. – *Ecol. Lett.* 9: 160–170.
- Thomsen, M. A., Corbin, J. D. and D'Antonio, C. M. 2006. The effect of soil N on competition between native and exotic perennial grasses from northern coastal California. – *Plant Ecol.* 186: 23–35.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. – *Proc. Natl Acad. Sci.* 101: 10854–10861.
- Weiss, S. B. 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. – *Conserv. Biol.* 13: 1476–1486.
- Zar, J. H. 1999. *Biostatistical analysis*. – Simon and Schuster.