Patterns of invasion within a grassland community

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Summary

1 Relatively few studies have looked for patterns of invasion by non-native species within communities. We tested the hypotheses that: (i) some types of microhabitats within a community are more invasible than others; (ii) microhabitat types that differ in invasion also differ in resource availability; and (iii) invasibility is mediated by effects of these resources on competition between native and non-native species.

2 To test the first two hypotheses, we measured plant cover and soils in a coastal grassland in northern California. Consistent with these hypotheses, cover of non-native plants was consistently high where nitrogen-fixing shrubs had recently grown, in the bottoms and sides of gullies and on deep soils, and these microhabitats tended to have relatively high nitrogen or water availability.

3 Cover and number of native species tended to be lower where cover of non-native species was higher, indicating that non-native species as a group negatively affected native species. However, the number of non-native species also tended to be lower where the total cover of non-natives was higher. This suggests that a few non-native species excluded natives and other non-natives alike.

4 To test the third hypothesis, we grew a common non-native, the annual grass Lolium multiflorum, and a common native, the perennial grass Hordeum brachyantherum, at different levels of water and nitrogen. The relative competitive ability of the native was higher at lower nitrogen availability but not at lower water availability. When 10-week-old native plants were grown with non-native seedlings and nitrogen was relatively low, the native out-competed the non-native. However, the non-native out-competed the native at all resource levels when species were both grown as seedlings. Competition between native and non-native grasses in this system may thus help prevent invasion by non-natives in microhabitats where nitrogen availability is low, but invasion may be relatively irreversible.

Key-words: invasive plant species, northern California coast, plant competition, soil characteristics, water and nitrogen availability


Introduction

The invasibility of natural communities, i.e. the likelihood that additional species will become established among the existing species in a habitat, has long been a central issue in ecology (e.g. Elton 1958). The accelerating spread of non-native species (Mooney & Hobbs 2000), defined as those carried by humans into a region (Randall 1997), offers an opportunity as well as a practical reason to study the factors that underlie invasibility.

Comparisons of the degree to which non-native plants have spread into different communities suggest that some types of communities or habitats are more invasible than others (e.g. Lonsdale 1999, Stohlgren et al. 1999). A wide range of factors may underlie these differences (e.g. D’Antonio et al. 1999; Alpert et al. 2000, Richardson et al. 2000a), including disturbance, resource availability, habitat fragmentation and accessibility, evolutionary history, propagule pressure, predation, mutualism and competition. These factors interact with each other and with the characteristics of individual species (Richardson et al. 2000b), making it difficult to identify the causes of invasibility in individual cases.
Experimental and inadvertent manipulations of resources provide additional evidence that availabilities of resources such as mineral nutrients and water are important determinants of the invasibility of communities by non-native plants. Adding nutrients to soils consistently promotes invasion (e.g. Wedin & Tilman 1996; Bakker & Berendse 1999). Adding water often promotes invasion (Milchunas & Lauenroth 1995; White et al. 1997), although decreasing water availability has been shown to promote invasion in at least one case (Cleverly et al. 1997). Other soil characteristics that influence resource availability, such as soil salinity, might thus also be expected to determine invasibility.

One mechanism by which high resource availability might increase invasibility is by increasing the ability of non-native plants to compete with natives. Garden and greenhouse experiments have shown that high nutrient or water availability can increase the ability of non-native plant species to compete with natives (Wedin & Tilman 1993; Nernberg & Dale 1997; Claassen & Marler 1998). Field experiments have shown interactive effects of resource availability and competition on invasibility (Burke & Grime 1996; White et al. 1997; Thompson et al. 2001).

Studying patterns of invasion within communities should be a good way to investigate the role of resource availability in invasion, as many of the other factors that may affect invasion, such as accessibility, history and predation, are likely to vary less within communities than between them. Relatively few studies (e.g. Hobbs & Mooney 1991, 1995; Roché et al. 1994; Stromberg & Griffin 1996; Hoopes & Hall 2002) have compared invasion between microhabitats within communities, but it is clear, for example, that woody, nitrogen-fixing plants can facilitate invasion by creating nitrogen-rich microsites (e.g. Vitousek & Walker 1989).

We compared the cover and species richness of native and non-native plants in a grassland community along the coast of northern California to test the hypothesis that: (i) differences in resource availability and soil characteristics between microhabitat types within communities and (ii) microhabitat types that differ in invasion also differ in resource availability or in soil characteristics likely to affect resource availability. We then conducted competition experiments based on the patterns of invasion and resource availability that we found to test the hypothesis that effects of resource availability on invasibility are mediated by their effects on the ability of native species to compete with non-native species.

**Methods**

**STUDY AREA**

Field research was conducted during June 1998 on Bodega Head, a small peninsula along the California coast about 80 km north of San Francisco. The peninsula rises up to 80 m in elevation and is composed of Mesozoic granitic rock partly overlain by Pleistocene deposits (Barbour et al. 1973). Soils are acidic, sandy and well-drained. Mean annual temperature is 11.7 °C, mean annual precipitation, entirely as rain, is 785 mm, and winds come predominantly from the west and northwest (Bodega Marine Laboratory, archived data available at www.bml.ucdavis.edu). Most of the rainfall (84%) occurs from November through March, and this largely determines the growing season for grassland herbs, which extends from November until June.

The natural vegetation on Bodega Head is primarily coastal prairie and coastal scrub, two community types characteristic of the coast of northern California (Heady et al. 1995). The coastal prairie at Bodega Head is dominated by native and non-native grasses, with scattered to locally dense stands of the shrubs Baccharis pilularis (nomenclature follows Hickman 1993) and Lupinus arboreus (bush lupine, referred hereafter as lupines). Shrubs of Lupinus create bare, nitrogen-enriched microsites in the grassland when they die (Maron & Jeffries 1999), and the percentage of species that are non-native is higher in microsites where lupines have recently died than in adjacent grassland (Maron & Connors 1996). We restricted our field surveys to areas where there was no known previous construction or agriculture. However, almost all of Bodega Head was probably grazed by sheep at times up until the mid-1960s, when use of the area was restricted to research and walking.

**FIELD MEASUREMENTS**

To test the hypothesis that degree of invasion differs between microhabitat types in the coastal prairie community on Bodega Head, we measured the cover of each vascular plant species in relation to distance from the ocean cliff edge, presence of dead remains of shrubs of Lupinus, topographic position in gullies, and patches of very shallow soil. We chose these factors because communications with Bodega Marine Reserve staff, preliminary inspections, and previous work on soil salinity (Barbour et al. 1973) and Lupinus (Maron & Connors 1996) at Bodega Head suggested that they might show the strongest relationships with invasion.

To test the effects of distance from the cliff edge, we located 50 × 50 cm plots at different distances from the cliff edge in two level sites, one behind the largest cove on Bodega Head (‘cove site’) and one on the nearest point (‘exposed site’). The cliff edge faced south-west at both sites. Transects at the exposed site paralleled a transect measured for soil salinity by Barbour et al. (1973), who found large differences in salinity over distances of tens of metres along their transect during the late spring. At each site, plots were placed at fixed distances (cove: 0, 2, 4, 10, 20, 30 and 40 m; exposed: 16, 36, 56 and 76 m) along six transects that started at random points along the cliff edge and ran perpendicular to inland. We chose the minimum and maximum distances at each site to avoid areas with stands of...
shrubs. We also incorporated a test of larger-scale distance from the ocean into our test of shallow vs. deep soils (see below).

To test the effects of past growth of *Lupinus*, we centered a plot on the remains of each of the 10 dead shrubs nearest to the plots at 30 and 40 m along the transects at the cove site, and compared plots with dead shrubs with the 10 nearest plots along transects. Dead shrubs consisted of partly broken canopies of bare, woody stems and main branches, which had little effect on light availability (Peter Alpert and Jonathan Blanchard, unpublished data). Work on lupine demography (Peter Alpert and Nathan Abare, unpublished data) suggested that these shrubs had died during the previous growing season.

To test the effects of topographic position in gullies, we randomly located eight 50 × 50 cm plots in each of three positions (bottom—slope < 5°; side—slope > 10°; shoulder—slope 5–10°) in the gully nearest the cove and the nearest gully of comparable size and aspect that was on the inland side of Bodega Head, near Bodega Bay. The first gully was selected so as to be relatively near other surveys and thus help make comparison between surveys more valid. The second gully was selected to replicate the first gully in topography but to potentially differ from it in microclimate and thus help test the generality of effect of topography in different gullies on Bodega Head.

To test the effects of patches of very shallow soil, we located 50 × 50 cm plots in four areas, each containing a cluster of one to three large shallow patches (> 5 mm diameter, < 25 cm in depth), as identified by probing the soil with a sharpened steel rod. These patches occurred on or near the tops of the small ridges and hills south of the cove, and appeared to be caused by the surface topography of the underlying bedrock. We systematically selected the two areas with shallow patches that were within 50 m of the cliff edge and that were nearest to the cove (‘ocean area 1’ and ‘ocean area 2’), and the two areas nearest to these that were within 50 m of the cliff edge (‘inland area 1’ and ‘inland area 2’). These areas lay near a longer transect measured for soil salinity by Barbour et al. (1973), who found large differences over the distance between the cove and inland areas. We located plots along random radii from the centre of each patch of shallow soil in each area, placing a ‘shallow’ plot along each radius at the point closest to half-way between the centre and edge of the patch where the soil was < 15 cm deep, and a ‘deep’ plot along each radius at the first place beyond the edge of the patch where the soil was > 60 cm deep. Replicates were distributed between patches in proportion to patch size: we measured 18 replicates at ocean 1, 12 at ocean 2, 12 at inland 1 and 8 at inland 2.

Cover of each vascular plant species in each plot was estimated visually according to a system of 14 cover classes (0–1, 1–5, 5–10, 10–15, 15–20, 20–25, 25–30, 30–40, 40–50, 50–60, 60–70, 70–80, 80–90 and 90–100% cover). In selected plots, the accuracy of these estimates was tested by comparing them with measurements of species occurrence at 100 points per plot. Visual estimates were generally within one cover class of point occurrence values and showed no tendency to be higher or lower. As June is probably the month when most of the grassland herbs set most of their seed, species abundance during June is likely to be related to seed production and plant fitness.

To test the hypothesis that microhabitats that differ in invasion differences in resource availability or in soil characteristics likely to influence resource availability, we measured soil water content, depth, pH and conductivity (as a measure of salinity) in plots where we measured plant species abundances. Because we had limited time and resources, we were able to measure only a subset of plots for water content, pH and conductivity, with an attempt to allocate measurements so as to provide the most information possible. We omitted soil measurements in plots with dead shrubs of *Lupinus*, based on the assumption that dead shrubs were not likely to affect soil depth, moisture, pH or salinity. We omitted measurements of water content, pH and conductivity at four intermediate distances along the cove site transects (2, 4, 10 and 30 m), and in randomly selected replicates in the test of shallow patches (nine replicates were measured at ocean 1, none at ocean 2, eight at inland 1, and five at inland 2). We were not able to measure soil nutrients and relied on previous studies (Maron & Connors 1996; Maron & Jefferies 1999) to demonstrate that soil nitrogen availability was relatively high under lupines.

We measured depth with a sharpened steel rod and recorded the mean of three measurements per plot. For the other soil measurements, we first collected and pooled three to five 10-cm-deep soil cores per plot. Cores were collected over as short a time interval as possible and by order of sets of replicates within each test (e.g. first replicate of each distance from cliff edge, second replicate, etc.). Each pooled sample was hand-cleaned of plant fragments and pebbles, weighed, dried at 60 °C for 72 h, and re-weighed to determine its water content. Although a single measure of water content is not a direct or absolute measure of water availability to plants, it is likely to provide a reasonable measure of relative water availability when soil texture and organic matter content are fairly homogeneous, which appeared to be the case in the grassland (Kolb 1999).

We then sieved each dried sample to remove particles > 2 mm and suspended a subsample of 25 g in 50 mL of distilled, de-ionized water. We stirred the suspension four times at 20–30-minute intervals, vacuum-filtered it (Rhoneads 1982), and measured it for electrical conductivity with an automatic, temperature-compensated conductivity meter (Hach CO150), and for pH with a standard glass electrode.

Like the measurements of soil water content, measurements of soil conductivity provided only a single-time comparison between plots. Both absolute levels
of salinity and differences between microhabitats in salinity have been shown to vary seasonally at Bodega Head (Barbour et al. 1973). Levels and differences tend to peak at the end of the dry season in October and November and to be least during January and February, two of the rainiest months. As the main growing season for herbs is from November through June, we probably measured salinity during the month of the growing season when levels and differences between habitats are likely to be greatest. Our results were thus likely to overrate rather than underestimate differences between microhabitats in soil salinity.

COMPETITION EXPERIMENTS

To test the hypothesis that effects of resource availabilities on invasibility are mediated by their effects on the ability of native species to compete with non-native species, we conducted two competition experiments between the second most common native species in our field plots, the perennial grass Hordeum brachyantherum (referred to as Hordeum), and the most common non-native species, the annual grass Lolium multiflorum (referred to as Lolium), at different levels of two resources that appeared to vary between microhabitat types with different degrees of invasion, nitrogen and water. We chose the second most common native species rather than the first, which was Bromus carinatus, because the abundance of Hordeum showed a stronger relationship to patterns of invasion (Kolb 1999).

In our first experiment, intended to mimic competition on bare ground or in heavily invaded microhabitats where Hordeum was absent, the species began competing as seedlings. In a second experiment, intended to at least partly mimic competition in less heavily invaded microhabitats where adult plants of Hordeum were present, we included treatments in which 10-week-old plants of Hordeum competed with seedlings of Lolium as well as treatments in which both species competed as seedlings. As 10-week-old plants were much younger than most established plants of Hordeum, results should underestimate the effect of life stage of Hordeum on competition with Lolium.

We collected seeds from Bodega Head in June 1998 and conducted experiments in a greenhouse at the University of Massachusetts during March to August 1999. Seeds were germinated in trays of sand. Approximately 10 days after germination, seedlings were transplanted into pots (6.4 cm in diameter by 25 cm deep) filled with acid-washed sand. For the first experiment, each species was grown in three competition treatments crossed with four resource treatments. The competition treatments were: plants grown singly (i.e. no competition, one plant per pot); monoculture (intraspecific competition, four plants of the same species per pot); and species grown together (mixed intra- and interspecific competition, two plants of each species per pot). The resource treatments were: high N (50 mg N L\(^{-1}\) nutrient solution); medium N (5 mg N L\(^{-1}\)); low N (1 mg N L\(^{-1}\)); and high N but low water (see below).

We selected the nitrogen levels so that the high and low levels would bracket the range of levels likely to occur in the grassland. We based the selection on the effects of a range of nutrient solutions on growth of a native species from the grassland, Fragaria chiloensis (Alpert 1991), the highest level caused plants of this species to grow much larger than they do in the grassland, and the lowest level supported survival but no net growth in biomass. Nitrogen was supplied as Ca(NO\(_3\))\(_2\) in a modified Hoagland's nutrient solution (Alpert 1991); concentrations of Ca\(^{2+}\) and of total ions were held constant in the different N treatments by appropriate additions of CaSO\(_4\). All pots were watered with nutrient solution (other treatments, in which plants grew more slowly), showing incipient wilting; enough solution was added at each watering to flush the soil and thus help avoid any build-up of nutrients. No water was added at any other time in the low water treatment but other pots were watered with tap water whenever the soil surface of any pot became dry.

We also included treatments at medium N and low water and at low N and low water. However, plants in these treatments did not grow enough to deplete the soil moisture, meaning that water levels were higher than in the high N, low water treatment. We therefore omitted these other low water treatments from the data analysis.

The singly grown plants and the plants grown in monoculture or species mixture were arranged in two separate randomized block designs to avoid edge effects between treatments with different plant densities. Each array had 10 blocks, each with one replicate of each treatment. Pots in the first array were spaced 8 cm apart to minimize shading. Pots in the second array were placed next to each other and surrounded by a border of edge pots also each planted with four plants.

After 9 weeks (plants grown singly) or 10 weeks (other treatments, in which plants grew more slowly), plants were harvested, divided into shoots and roots, dried to constant mass at 60 °C, and weighed. As plants were grown in sand, it was relatively easy to separate their roots from the soil and from each other. A small proportion of roots became detached during harvest and were not included in estimates of biomass.

For the second experiment, we used only the competition treatment in which species were grown together and grew plants at two nitrogen levels (high and medium, as above) crossed with two life stages of Hordeum (seedlings or 10-week-old plants). The older plants had been germinated at the same time as the seedlings for the first experiment and grown in the same greenhouse. Treatments were arrayed as in the second array in the first experiment, but with 11 blocks, and harvested after 9 weeks in August 1999.
**DATA ANALYSIS**

Before statistical analysis of the data, cover classes were converted to their midpoints, proportional data were transformed to the arcsine of the square root, and other data were log-transformed as needed to improve homoscedasticity and normality. We present only untransformed data in figures to best represent the actual values found in the field and the greenhouse. In cases where soil depth exceeded the length of the soil probe, effects of independent variables on soil depth were tested with Kruskal–Wallis tests. We tested effects of independent variables on the cover and species richness of natives and non-natives and on soil characteristics with analysis of variance (ANOVA) in SYSTAT 9.0 or SAS 6.12. We used one-way ANOVA and posthoc Tukey tests to analyse the effects of distance from the ocean and of *Lupinus*, two-way ANOVA and orthogonal contrasts (single degree of freedom tests, using the *Hypothesis* function in SYSTAT) to test effects of topographic position in gullies and of gully, and a mixed ANOVA model with area (i.e. cluster of shallow soil patches) nested within distance of area from the ocean to test effects of shallow vs. deep soil, area, and distance of area from the ocean.

To analyse the first competition experiment, we used three-way ANOVAs to test effects of competition, species and resource availability (water or N) on total plant dry biomass in the monoculture and mixed species treatments, and two-way ANOVAs to test effects of species and resource availability on the total mass of singly grown plants. In the mixed species treatment, we used means of the two plants of the same species in each pot in analyses. In the monoculture treatment, we used means of the mass of two randomly chosen plants per pot. Pots in which any plants died were excluded from analysis. To analyse the second competition experiment, we used a two-way ANOVA to test the effects of N and life stage of *Hordeum* on the relative performance of *Hordeum* (mass of *Hordeum* per pot divided by total plant mass per pot).

**Results**

**PATTERNS OF INVASION**

**Dead shrubs of *Lupinus***

Grassland with remains of dead shrubs of *Lupinus arboreus* was more highly invaded than adjacent grassland without shrubs or remains of dead shrubs (mean cover of non-natives [with SE in brackets] = 94.0 [4.8]% in plots with dead *Lupinus* vs. 71.0 [7.2]% in plots without *Lupinus*; *F*$_{1,42}$ = 8.19, *P* = 0.04). In contrast, cover and species richness of natives were lower in the plots with dead *Lupinus* (cover − 5.5 [1.3] vs. 21.5 [4.8]%); *F*$_{1,42}$ = 8.75, *P* = 0.008; species richness − 1.5 [0.2] vs. 4.1 [0.5] species per 0.25 m$^2$ plot; *F*$_{1,42}$ = 20.56, *P* < 0.001). This suggested that non-natives had partly excluded natives from plots under dead shrubs. Surprisingly, species richness of non-natives was also lower in plots with dead *Lupinus* (3.4 [0.4] vs. 6.9 [0.7] species per 0.25 m$^2$ plot; *F*$_{1,20}$ = 15.81, *P* = 0.001), suggesting that invasion by some non-natives had excluded other non-natives.

**Gullies**

The bottoms and sides of gullies were more invaded than their shoulders (Fig. 1a; effect of topographic position on cover of non-natives: $F_{1,42}$ = 45.51, *P* < 0.001). As in the case of dead shrubs of *Lupinus*, cover of natives (Fig. 1a) did show a significant effect of position: $F_{1,42}$ = 57.67, *P* < 0.001 and species richness of natives (Fig. 1b; $F_{1,42}$ = 34.87, *P* < 0.001) tended to be lower where the cover of non-natives was higher. Species richness of non-natives showed no consistent pattern with respect to position in the gullies (Fig. 1b), even though it did show a significant effect of position across gullies ($F_{1,42}$ = 7.26, *P* < 0.002).

There was relatively little difference between gullies in overall degree of invasion. Across positions, cover of non-natives was marginally higher in the gully near the bay than in the gully near the cove (Fig. 1a; effect of gully: $F_{1,42}$ = 4.27, *P* = 0.04), while cover of natives was slightly lower in the gully near the bay ($F_{1,42}$ = 6.56; *P* = 0.01). Species richness did not differ between gullies (Fig. 1b; *P* > 0.2 for both non-natives and natives).
More invaded topographic positions within gullies tended to have lower soil conductivity and deeper soil: conductivity was lower and soil depth was greater in the bottoms than on the shoulders of gullies (Table 1). Invasion in gullies showed no consistent relationship to soil water content or pH. In one gully, water content and pH varied little between positions (Table 1). In the other gully, water content was higher and pH was very slightly but statistically significantly lower on the bottom and side than on the shoulder, that is, where invasion was greater.

Shallow soil

Very shallow soil was less invaded than adjacent, deeper soil in three of the four areas with shallow soil patches that were sampled (Fig. 2a; effect of depth x area on cover of non-natives: $F_{3,42} = 8.34, P < 0.001$). As in the cases of dead Lupinus and position in gullies, the cover (Fig. 2a) and species richness of natives (Fig. 2b) were higher where the cover of non-natives was lower. Cover of natives was higher on shallow soils in the same three areas where cover of non-natives was lower (effect of depth: $F_{1,42} = 20.92, P = 0.04$). Species richness of non-natives was higher on shallow soils across all areas (effect of depth: $F_{1,42} = 160.90, P = 0.006$). Distance of an area from the ocean had no effect on

![Table 1](image)

<table>
<thead>
<tr>
<th>Topographic position</th>
<th>Water content (g H$_2$O 100 g$^{-1}$ soil)</th>
<th>Conductivity (dS m$^{-1}$)</th>
<th>pH</th>
<th>Depth (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gully near the cove</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shoulder</td>
<td>9.4 (0.4)</td>
<td>0.22 (0.02)</td>
<td>5.7 (0.04)</td>
<td>85 (14)</td>
</tr>
<tr>
<td>Side</td>
<td>13.5 (0.6)</td>
<td>0.21 (0.03)</td>
<td>5.5 (0.04)</td>
<td>&gt; 175</td>
</tr>
<tr>
<td>Bottom</td>
<td>15.6 (1.3)</td>
<td>0.18 (0.01)</td>
<td>5.5 (0.07)</td>
<td>&gt; 175</td>
</tr>
<tr>
<td>Gully near the bay</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shoulder</td>
<td>8.6 (0.5)</td>
<td>0.15 (0.009)</td>
<td>5.5 (0.05)</td>
<td>85 (14)</td>
</tr>
<tr>
<td>Side</td>
<td>8.1 (0.4)</td>
<td>0.09 (0.008)</td>
<td>5.5 (0.05)</td>
<td>&gt; 175</td>
</tr>
<tr>
<td>Bottom</td>
<td>7.6 (0.5)</td>
<td>0.09 (0.004)</td>
<td>5.5 (0.05)</td>
<td>&gt; 175</td>
</tr>
</tbody>
</table>

ANOVA d.f. $F_{1,42}$ $P$ $F_{1,42}$ $P$ $F_{1,42}$ $P$

- Gully 1 70.50 < 0.001 55.98 < 0.001 1.92 0.2
- Position 2 7.46 0.002 5.74 0.006 5.01 0.01
- Gully x position 2 13.91 < 0.001 1.58 > 0.2 3.98 0.01
Invasion differed between soil depths (all \( P > 0.2 \)). The difference between areas in the degree to which invasion differed between soil depths appeared to be related to the depth of the deep soils in each area. Areas showed significant differences in how much soil depths varied between the shallow and deep plots in an area (Table 2: effect of depth × area). Thus, the area in which the deep soils were least deep (inland area 2) was the one area that showed no difference between shallow and deep soils in degree of invasion (Fig. 2). This provided further evidence that soil depth strongly determined invasion.

Among soil characteristics other than depth, pH showed the closest relationship to degree of invasion on shallow vs. deep soils. Shallow soils tended to have a slightly lower pH than deeper soils (Table 2: effect of depth × area), especially in the two areas that were measured for pH and also showed less invasion on shallow than on deep soil (ocean area 1 and inland area 1 but not inland area 2). Shallow soils were marginally lower in water content than deep soils (Table 2: effect of depth). Soil conductivity was higher on shallow soil only in the area where shallow soils were not markedly less invaded (Table 2: effect of depth × area within distance).

### Individual species

Some individual native and non-native species deviated from the patterns of abundance shown by natives and non-natives as groups. We illustrate this by comparing the cover of the five most common species, two natives and three non-natives, on the shallow and deep soils (Fig. 3). Averaged across the four areas measured, cover of one of the native species (Bromus carinatus) was higher on the deeper soils, in contrast to the pattern for total cover of all natives (Fig. 2). Cover of two common non-native species, like the pattern for total cover (Fig. 2), was higher on deeper soils, but for the third common and all of the less common non-natives combined (Fig. 3: ‘other’ non-natives), cover was higher on shallow soils. Some natives were thus more abundant where invasion was greater, and most non-natives were more abundant where invasion was less, despite patterns of total native and non-native cover being in the opposite direction. Complete data on abundances of individual species in all plots in the study are given in Kolb (1999).

### Distance from the cliff edge

Along transects, distance from the cliff edge had no consistent effect on invasion (data not shown). At the exposed site, distance did not affect cover of non-native species (\( F_{1,38} = 2.56, P = 0.08 \)). At the cove site, distance did affect non-native cover (\( F_{5,38} = 8.45, P < 0.001 \)): cover at the greatest distance, 40 m, exceeded

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### Table 2

Characteristics (mean (SE)) of soils from shallow patches and of adjacent deeper soils on Bodega Head, measured in June 1998. Values of \( P \) are in italics if \( P < 0.05 \).

<table>
<thead>
<tr>
<th>Area</th>
<th>Water content (g H₂O 100 g⁻¹ soil)</th>
<th>Conductivity (dS m⁻¹)</th>
<th>pH</th>
<th>Depth (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ocean area 1:</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Shallow</td>
<td>9.5 (0.7)</td>
<td>0.35 (0.02)</td>
<td>5.5 (0.03)</td>
<td>13 (1)</td>
</tr>
<tr>
<td>Deep</td>
<td>13.9 (0.4)</td>
<td>0.33 (0.02)</td>
<td>6.0 (0.05)</td>
<td>106 (4)</td>
</tr>
<tr>
<td>Ocean area 2:</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Shallow</td>
<td>8.7 (0.4)</td>
<td>0.19 (0.02)</td>
<td>5.2 (0.05)</td>
<td>12 (1)</td>
</tr>
<tr>
<td>Deep</td>
<td>11.8 (0.5)</td>
<td>0.19 (0.01)</td>
<td>5.3 (0.03)</td>
<td>110 (7)</td>
</tr>
<tr>
<td>Inland area 1:</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Shallow</td>
<td>8.8 (0.4)</td>
<td>0.28 (0.01)</td>
<td>5.2 (0.05)</td>
<td>10 (1)</td>
</tr>
<tr>
<td>Deep</td>
<td>13.1 (0.2)</td>
<td>0.19 (0.01)</td>
<td>5.3 (0.05)</td>
<td>78 (5)</td>
</tr>
<tr>
<td>Inland area 2:</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Shallow</td>
<td>8.8 (0.4)</td>
<td>0.26 (0.01)</td>
<td>5.2 (0.05)</td>
<td>110 (7)</td>
</tr>
<tr>
<td>Deep</td>
<td>13.1 (0.2)</td>
<td>0.19 (0.01)</td>
<td>5.3 (0.05)</td>
<td>78 (5)</td>
</tr>
</tbody>
</table>

**ANOVA**

- Depth: \( F_{1,38} = 69.99, P = 0.001 \)
- Distance: \( F_{1,38} = 4.04, P = 0.05 \)
- Area (within distance): \( F_{1,38} = 1.25, P = 0.25 \)
- Depth × distance: \( F_{1,38} = 0.52, P = 0.25 \)
- Depth × area (within distance): \( F_{1,38} = 1.37, P = 0.25 \)

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To elaborate: Fig. 3 shows the cover of five common species (mean ± SE based on means in each of four areas measured) on shallow and adjacent deep soils. Symbols give the probability that cover did not differ between shallow and deep soil: NS > 0.5, *< 0.05, **< 0.01, ***< 0.001 (results from ANOVA). Upper, middle and lower symbols give effects of depth, depth × distance, and depth × area within distance, respectively. Species: Hordeum bradyantherum, Bromus carinatus, Vulpia bromoides, Holcus lanatus and Lolium multiflorum.
Effects of nitrogen and water availability on mean plant growth of Hordeum brachyantherum and Lolium multiflorum

In the first greenhouse experiment, in which the native, perennial grass *Hordeum brachyantherum* and the non-native, annual grass *Lolium multiflorum* were both started from seedlings, singly grown plants of *Hordeum* accumulated less mass than singly grown plants of *Lolium* in all resource treatments (Fig. 4a; two-way ANOVA of total mass of singly grown plants at different levels of N: effect of species, $F_{1,70} = 17.63, P < 0.001$; ANOVA at different levels of water: effect of species, $F_{1,70} = 18.48, P < 0.001$). Moreover, the effects of resource treatments on singly grown plants did not differ significantly between species (effect of species $\times$ N, $F_{1,36} = 0.38, P > 0.2$; effect of species $\times$ water, $F_{1,36} = 0.92, P > 0.2$). In the absence of competition, the native thus grew less than the non-native and showed no difference from the non-native in ability to tolerate low nitrogen or low water availability.

Species differed strongly in their responses to intraspecific competition (Fig. 4b) as compared with intra-plus interspecific competition (Fig. 4c; three-way ANOVA of total mass of plants grown in monoculture or species mixture at different N levels: effect of species $\times$ competition, $F_{1,36} = 25.73, P < 0.001$; ANOVA at different water levels: effect of species $\times$ competition, $F_{1,36} = 73.07, P < 0.001$). Plants of *Hordeum* accumulated more biomass in monoculture than in species mixture, whereas the reverse was true for *Lolium*. This indicated that *Lolium* was the better competitor when the species competed as seedlings, even when availability of nitrogen or water was low.

Nitrogen availability modified the relative effects of intra- and intra-plus interspecific competition on the two species (effect of species $\times$ competition $\times$ N, $F_{2,70} = 4.39, P = 0.02$): the difference between total mass in monoculture and in species mixture was less at lower nitrogen for both species (Fig. 4b,c). In contrast, water availability had only a marginally significant effect on the difference in the response of the species to types of competition (effect of species $\times$ competition $\times$ water: $F_{1,70} = 3.55, P = 0.06$). Moreover, the nominal effect of water was opposite to that of nitrogen: the difference between total mass in monoculture and in species mixture was greater at lower water for both species (Fig. 4b,c). These results indicated that low nitrogen availability increased the competitive ability of the native relative to the non-native, whereas low water availability did not. Competition also induced differences between species in their ability to maintain growth at low nitrogen: in species mixture, the native species tolerated low nitrogen better than the non-native (Fig. 4c).

Effects of nitrogen availability and life stage on outcome of competition between *Hordeum brachyantherum* and *Lolium multiflorum*

Although reduced levels of nitrogen increased the ability of *Hordeum* to compete with *Lolium* when both species were planted as seedlings, *Hordeum* still made up less than half of the final total biomass per pot in all treatments in the first experiment (Fig. 5a). The biomass of *Hordeum* was significantly less than that of *Lolium* (each $P$ [orthogonal contrast] < 0.05) at all but...
Patterns of invasion

Results provided some support for the hypothesis that microhabitat types that differ in invasibility also differ in resource availability. Patches left by dying shrubs of Lupinus are relatively high in nitrogen (Maron & Connors 1996; Maron & Jeffries 1999). This suggests a relationship between high nitrogen and high invasibility, although patches left by shrubs are also initially high in light availability. Deeper soils tended to be higher in water content and slightly less acidic than soils on shallow patches, suggesting a positive relationship between water availability and invasion, and a negative relationship between acidity and invasion. Soil salinity was higher nearer the cliff edge along transects, in areas of shallow patches nearer the ocean, and on the shoulders as compared with the bottoms of gullies. This suggests that salinity is higher in microhabitats that are more exposed to ocean aerosols, consistent with the findings of Barbour et al. (1973), but distance from the ocean showed no relationship to invasion. Results therefore suggest only that nitrogen and water availability could be related to invasion in the grassland.

**EFFECTS OF NON-NATIVES ON NATIVES**

The spread of non-native plants appears to have had a significant negative effect on the native plants of Bodega Head. With few exceptions, both cover and species richness of natives were lower in microhabitats where the cover of non-natives was higher. However, invasion by non-native plants also appears to have had a negative effect on other non-natives. Thus, the species richness of non-natives was generally lower where their cover was higher. Although there was inverse variation between cover of natives and non-natives, there was parallel variation in species richness of natives and non-natives. A likely explanation is that invasion by a few non-native species reduces the abundance of the majority of the other non-natives, as well as of the native species in the grassland.

**THE ROLE OF COMPETITION**

The effects of low nitrogen and low water availability on competition between the native grass *Hordeum*

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Patterns of invasion

**Fig. 5** Relative performance of *Hordeum brachyantherum* (mass of *Hordeum* per pot/total plant mass per pot; mean ± SE) when grown together with *Lolium multiflorum* at different levels of resource availability. Nitrogen levels: H* = high but with low water, H = high, M = medium, L = low. (a) First experiment, with both species planted only as seedlings (one-way ANOVA: effect of N [treatments H, M and L], F\(1,18\) = 5.34, P = 0.01; effect of water [treatments H* and H], F\(1,18\) = 3.21, P = 0.09); (b) second experiment, with *Hordeum* planted either as seedlings or as 10-week-old plants, and *Lolium* planted only as seedlings (two-way ANOVA: effect of N [treatments H and M], F\(1,18\) = 19.7, P < 0.001; effect of life stage of *Hordeum* [seedling or 10-week-old plant], F\(1,18\) = 154.7, P < 0.001; effect of N × life stage – F\(1,18\) = 1.82, P = 0.19).

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The lowest N level (P = 0.08). *Lolium* thus out-competed *Hordeum* at all water and nitrogen levels when both species competed as seedlings.

When *Hordeum* was planted as 10-week-old plants and *Lolium* as seedlings in the second experiment (Fig. 5b), *Hordeum* made up about half of the biomass per pot at high N and much more than half at medium N. The combination of reduced nitrogen and prior establishment thus did enable *Hordeum* to out-compete *Lolium.*

**DISCUSSION**

**PATTERNS OF INVASION**

Results generally supported the hypothesis that degree of invasion would differ between types of microhabitats within the grassland community. Of the four patterns tested, three showed significant effects of microhabitat type on cover of non-native plant species: invasion was relatively high under dead shrubs of *Lupinus,* in the bottoms and sides of gullies, and away from patches of shallow soil, but did not depend upon distance from the ocean cliff edge. These results indicated that invasibility can vary substantially within a community even where soil type and texture vary little. Results also highlight the potential importance of soil depth as a determinant of invasibility, as patterns of invasion on patches of shallow soil, in gullies and on the deeper soil in different areas were all associated with soil depth. The few comparable studies on patterns of invasion within grassland communities in the region suggest that soil depth may also be related to invasion in other grasslands. Murphy & Ehrlich (1989) noted that remnants of native grassland in California tend to be found on shallow soils on exposed slopes. Roché et al. (1994) found that invasion by *Centaniera solstitialis* in grasslands in eastern Washington was greatest on slopes with deep soils. Our surveys of invasion in gullies and on shallow patches suggest that soils > 90 cm deep are more prone to invasion than less deep soils in the coastal prairie at Bodega Head.

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brachyantherum and the non-native grass *Lolium multi-florum* partly supported our third hypothesis, that effects of resource availability on invasibility are mediated by their effects on the ability of native species to compete with non-native ones. Low nitrogen increased the ability of *Hordeum* to compete with *Lolium*, but low water availability did not.

The shift in relative competitive ability due to nitrogen availability was unrelated to the ability of each species to tolerate low nitrogen availability in the absence of interspecific competition; the native showed a greater ability than the non-native to maintain growth at low nitrogen only when the species were grown together. Competition experiments in which five native and non-native grasses from Bodega Head were grown together and separately at high and low nitrogen availability also showed that the species had similar tolerance levels and that the natives were already established, but not when all the species were grown together (Jennifer M. Benson & T. Joseph Barone, unpublished data). Species interactions can thus induce differences between native and non-native species in ability to tolerate low resource availability.

*Hordeum* seedlings were unable to out-compete *Lolium* seedlings at any resource level. As *Hordeum* is a perennial and *Lolium* is an annual, the species should compete entirely as seedlings only in grassland where adults of *Hordeum* are absent, as is the case at Bodega Head in highly invaded microhabitats or in patches laid bare by disturbance or death of shrubs. This suggests that the re-establishment of *Hordeum* in microhabitats from which adult plants have been eliminated may be very slow if seeds of *Lolium* are present. *Hordeum* did out-compete *Lolium* when 10-week-old plants of *Hordeum* competed with seedlings of *Lolium*, provided that nitrogen availability was not high. *Hordeum* may thus be able to prevent or slow invasion by *Lolium* into microhabitats where there are established populations of *Hordeum*, as long as nitrogen availability is not elevated.


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References


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