

# A California grasslands alkali specialist, *Hemizonia pungens* ssp. *pungens*, prefers non-alkali soil

Veblen Kari E.<sup>1,2\*</sup> & Young Truman P.<sup>2</sup>

<sup>1</sup>Ecology Graduate Group, University of California, Davis, CA 95616, USA;

<sup>2</sup>Department of Plant Sciences, University of California, Davis, CA 95616, USA; E-mail tpyoung@ucdavis.edu;

\*Corresponding author; Fax +1 530 752 1819; E-mail keveblen@ucdavis.edu

## Abstract

**Question:** Edaphically severe habitats commonly support edaphic endemics, specialized plant species that do not occur elsewhere. The endemism of native plant species in edaphically specialized habitats suggests either (a) that these native endemic species are uniquely specialized to survive and grow better under the conditions prevalent in these harsh areas, or (b) that these areas represent refuges from competition with other (often exotic) species.

**Location:** Central Valley, California, USA.

**Methods:** We surveyed the vegetation distribution in alkali sinks and carried out a reciprocal transplant greenhouse experiment crossed with a competition treatment to examine the interplay between interspecific competition and edaphic factors in determining relative performance of an alkali endemic forb (*Hemizonia pungens* ssp. *pungens*) and its exotic grass competitor (*Lolium multiflorum*).

**Results:** *Lolium* consistently performed better in non-alkali soil. In contrast, *Hemizonia*, in the absence of competition, performed significantly better on the non-alkali soils, but in competition with *Lolium*, performed equally well on alkali and non-alkali soils.

**Conclusions:** These results suggest that *Hemizonia* does not inherently prefer harsh alkali soil, but is better able to tolerate alkali soil and may be excluded from more moderate soils by competition. Therefore, edaphic and biotic effects may interact to determine the spatial distribution of this edaphic endemic. Our data suggest a mechanism by which competition between native and exotic species on impoverished soils leads to dominance of native species and creation of refugia for native species where exotic species are unable to thrive.

**Key words:** Abiotic; Alkali sinks; Context-dependent competition; Edaphic mosaic; Refuge hypothesis; Ryegrass; Tar plant.

## Introduction

One of the primary goals of ecology is determining factors that affect the distribution and abundance of species. Distributions of plant popu-

lations are limited by a combination of biotic factors, such as competition, and abiotic factors, such as edaphic conditions. Understanding the relative contributions of these limiting factors is especially interesting when considering observed patterns of “edaphic endemism”.

Edaphically severe habitats commonly support edaphic endemics, specialized plant species that do not occur elsewhere. Examples of edaphic endemism include serpentine outcrops (Gram et al. 2004; Brady et al. 2005; Harrison et al. 2006), limestone and calcareous soils (Xu 1995; Danin 1999; Cremene et al. 2005), vernal pools (Gerhardt & Collinge 2003; Zedler 2003), and desert springs (Tiner 2003). These habitats tend to support isolated populations, patchily distributed in the landscape, with the potential to greatly contribute to both local and regional diversity.

Patches of edaphic endemism also frequently exist as refuges for native species in highly invaded ecosystems. For example, although California’s grasslands are severely invaded by exotic annual plants, native plant species often survive in edaphically severe habitats that are more resistant to invasion (vernal pools, serpentine outcrops, alkali sinks, shallow soils on hardpan) (e.g. Williamson & Harrison 2002; Gerhardt & Collinge 2003; Harrison et al. 2006). This pattern has led to interest in the roles of competition and edaphic factors as determinants of invasion success (Huenneke et al. 1990; Hoopes & Hall 2002).

The endemism of specialized plant species in edaphically severe sites suggests either that (a) edaphic endemics are so specialized for growth under the conditions prevalent in these areas that they perform inherently better than in more moderate soil conditions, or (b) these areas represent refuges from competition with other plant species (Hoopes & Hall 2002; Williamson & Harrison 2002), which, in California grasslands, often are exotic annual grasses. Evidence from other ecosystems suggests

that, for some species, stressful environments may serve as refuges from competition (Wilson & Keddy 1986; Pugnaire & Luque 2001; Liancourt et al. 2005). Over 50 years ago, Kruckeberg (1954) hypothesized that the restriction of serpentine endemics was not due to an inherent preference of these species for the severe edaphic conditions on serpentine soils, but rather that “serpentine endemics are able to maintain themselves in open serpentine communities where competition is not severe, but not in the more rigorous competition of non-serpentine soils” (Kruckeberg 1954: p 272). He then provided experimental evidence that this was indeed the case. Since then, there have been few experimental examinations of these patterns and no formal tests of the refuge hypothesis. Jurjavcic et al. (2002) found conflicting experimental patterns of competition and tolerance on serpentine soils in *Vulpia microstachys*, which is not a serpentine specialist. Hart (1980) found results suggestive of a refuge effect in serpentine outcrops, but did not directly test this effect. In the context of alkali sinks and alkali endemics, Hoopes & Hall (2002) presented experimental evidence merely suggestive of the refuge effect in *Sporobolus airoides* (alkali sacaton). In contrast, Wright et al. (2006) presented evidence from a reciprocal transplant experiment that the serpentine ecotype of *Collinsia sparsiflora* did indeed perform better on serpentine soils than on non-serpentine soils, even in the absence of competition. Therefore, both the refuge hypothesis and the edaphic preference hypotheses remain viable alternatives for explaining edaphic endemism, and the answers may well be species- and site-specific. Here, we present evidence from an experimental test of the hypothesis that the restriction of individuals of the alkali endemic *Hemizonia pungens* ssp. *pungens* (Hook and Arn.) Torr. and Gray is not due to a preference for strongly alkali soils, but rather to the refuge from competition provided by these soils.

We surveyed vegetation distribution in alkali sinks and carried out a reciprocal transplant greenhouse experiment crossed with a competition treatment to examine the interplay between interspecific competition and edaphic factors in determining relative fitness of an alkali endemic forb (*Hemizonia pungens* ssp. *pungens*) and its exotic grass competitor (*Lolium multiflorum* Lam.). We tested two competing hypotheses: (a) that *Hemizonia* would grow better on alkali soil than on non-alkali soil when grown without competition, and (b) that *Hemizonia* would grow better on non-alkali soil than on alkali soil, but only in the absence of competition.

## Methods

### *Study site and focal species*

Vernal alkali sinks embedded in impeded drainage grasslands in Yolo County, in the Central Valley of California, provided a natural edaphic mosaic in which to study local endemism. These seasonal wetlands flood during winter rains, leading to saline-alkali soils of low productivity that support unique specialist plant species. These areas are of conservation priority due to their rarity and high plant endemism (Anon. 2001).

Our study area was a seasonally inundated pasture with scattered alkali sinks (25–200 m<sup>2</sup>) located in Yolo County, CA (38°37'N, 121°43'W), approximately 10 km northwest of Davis, now part of the Alkali Grasslands Reserve. These sinks are part of a series of alkali sinks in this area that appear to be of geologic origin (M. Singer, pers. comm.), and they host a number of rare and endemic alkali specialists (Anon. 1996). In our study area, the native alkali specialist, *Hemizonia pungens* ssp. *pungens* dominates these sinks, with the surrounding matrix dominated by the invasive exotic *Lolium multiflorum*.

*Hemizonia pungens* is an annual composite, native to interior grasslands of the Pacific coast. The subspecies *H. pungens* ssp. *pungens* is endemic to the Central Valley of California (Hickman 1993). The annual grass *Lolium multiflorum* was first introduced to the United States in the late 1600s and repeatedly thereafter, and has since become well established in much of the United States, including California's grasslands. It is intentionally seeded for revegetation and livestock forage (e.g. Hannaway et al. 1999), but is also known to be invasive and difficult to eradicate. The reported pH tolerance range of *Lolium* is 5–7.8 (Hannaway et al. 1999). It does poorly in excessively or poorly drained soils, but can survive in the latter if it is well established and temperatures are low (Hannaway et al. 1999). Despite these limitations, *Lolium* appears to threaten endangered vernal pools in California (Anon. 1999), and we have observed what appear to be early stages of invasion into alkali sinks (Dawson et al. 2007).

### *Soil and vegetation surveys*

In May 2005, we surveyed four alkali pools. There was no longer standing water in the pools at the time of the survey, but the plants were still fully green. Pools were identified by local topography, *Hemizonia* dominance, and (salt-encrusted) bare

ground, while non-pools were areas of dense *Lolium* monoculture. At each of four pools, we placed three 1 m×1 m quadrats in each of three microsites: pool, edge, and background (non-pool), for a total of 36 quadrats. In each quadrat, we placed a ten-point pin frame, and counted total hits for each plant species. We also estimated the percentage of *Hemizonia* plants that were flowering. At each pool and background microsite, we collected one soil sample from 0-10 cm (eight soil samples total) and air-dried all samples. We measured pH of these samples in the lab in a 1:1 ratio of soil to deionized water. The UC Davis DANR soils laboratory analyzed the soil samples for total sodium, ammonium nitrogen, nitrate nitrogen, potassium, calcium, and magnesium. Pools were surveyed for maximum water depth at the height of the rainy season in February 2006.

#### *Greenhouse reciprocal transplant experiment*

We collected soil for experimental planting from the upper 30 cm inside the alkali area (pH 8.5, measured on-site with field pH tester and in the laboratory with 1:1 ratio of soil to deionized water), and in the area outside and adjacent to the alkali area (pH 7.3) in May 2004. To prepare soil for planting, we crushed the soil through a 1–2-mm sieve. The soil was put in an oven for 48 h (at 60°C) to kill seeds. We then placed soil into 10 cm×10 cm×10 cm pots and treated it with 0.02% polyacrylamide (PAM), a linear polymer, to stabilize soil structure; without the polymer, infiltration would have been severely impeded because of the high clay content of the soil and behavior of high clay soils in pots. The treated soil was then put in an oven again for 24 h.

During May and June 2003, we collected *Hemizonia* seed from randomly selected plants growing inside the alkali sinks and *Lolium* seed from plants growing inside and outside the sinks. Seeds were stored in envelopes at room temperature for 7 months. Based on results of earlier germination trials, we soaked *Hemizonia* seeds in 10% bleach solution for 5 min, then in deionized water for 5 min. We then stratified the seeds for 18 days by placing them between wet paper towels in plastic bags stored at 10°C. *Lolium* seeds were similarly soaked in bleach solution and deionized water, but did not need stratification. In April 2004, we seeded *Hemizonia* at a rate of 25 seeds pot<sup>-1</sup>, and *Lolium* 1 week later (to synchronize seedling emergence) at a rate of 10 seeds pot<sup>-1</sup>.

Sixty pots were arranged on a greenhouse mist bench at UC Davis in a full-factorial randomized

complete block design. In each of ten blocks, we crossed two levels of competition (interspecific competitor present versus absent) with two soil types (alkali soil versus non-alkali soil) for each species. By “non-alkali” here (and throughout), we mean considerably less alkali soils in the grassland matrix, which were still slightly basic. Plant-soil treatment combinations were: (1) *Hemizonia* only, alkali soil, (2) *Hemizonia* only, non-alkali soil, (3) *Lolium* only, alkali soil, (4) *Lolium* only, non-alkali soil, (5) *Hemizonia*+*Lolium*, alkali soil, (6) *Hemizonia*+*Lolium*, non-alkali soil.

For the first 3 weeks, water was given to all seed trays when needed, and we rotated positions of blocks on the mist bench to minimize effects of uneven misting. We assessed percentage germination 10 days after planting. Due to patchier and lower than expected *Hemizonia* germination, we then transplanted from pots of higher germination to pots of lower germination (of the same soil type), so that each *Hemizonia* and *Hemizonia*+*Lolium* pot had between one and five *Hemizonia* plants. *Lolium* were thinned to match the number of *Hemizonia*. Plants survived throughout the experiment in all pots except one “*Lolium* only, non-alkali soil” pot. We chose height as our performance metric, measured from base to tip of the tallest tiller for *Lolium* and from base of stem to apical bud for *Hemizonia*, after 3 weeks and after 6.5 weeks. We also counted number of leaves (not including cotyledons). Flowering was limited in the time frame of this experiment. We conducted a greenhouse (instead of field) experiment because our experimental question would have required the intentional introduction of an exotic invasive species into uninvaded native alkali sink vegetation.

#### *Statistical analyses*

We performed one-way ANOVAs to test for soil and vegetation differences between alkali pool and non-pool areas. Soil response variables were pH, sodium, ammonium nitrogen, nitrate nitrogen, potassium, calcium, and magnesium. Vegetation response variables were cover of each species and percentage flowering.

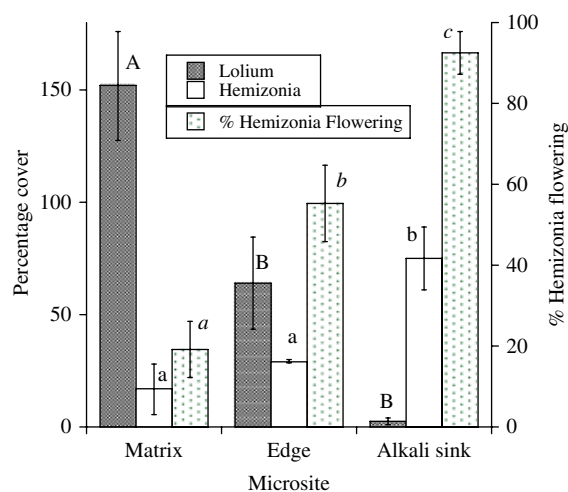
We used repeated measures ANCOVA to assess the effects of interspecific competition and soil type on greenhouse seedlings at 3 weeks and 6.5 weeks. For each response variable for each plant species, we included block, soil type (alkali versus non-alkali), interspecific competition (presence versus absence), and soil type×interspecific competition as factors in our model. Number of competitors (ranging from

one to five) was treated as a covariate. Response variables for both *Lolium* and *Hemizonia* were height at 3 and 6.5 weeks. To test our two hypotheses, class means were compared with planned independent orthogonal contrasts. This statistical model was also used to test number of leaves and germination percentage, although germination excluded number of competitors as the covariate. Although we do not know whether height provides a reliable estimate of relative performance across species, we performed an additional analysis to compare final height of both species; model effects were focal species (*Hemizonia* versus *Lolium*), soil, competition, soil  $\times$  competition interaction, and number of competitors as the covariate. Independent contrasts were used to test our hypotheses that *Hemizonia* out-competed *Lolium* in alkali soil and vice-versa on non-alkali soil.

## Results

### Soil and vegetation surveys

Our vegetation sampling quantified the differences in species' abundances and performance between pool and non-pool sites. *Hemizonia* abundance was five times higher inside pools than in the surrounding matrix ( $P < 0.05$ ), and *Lolium* was abundant in the matrix, but rare in the pools ( $P < 0.05$ , Fig. 1). Few *Hemizonia* individuals outside the pools flowered, compared to nearly 100%



**Fig. 1.** Quantification of visual differences between alkali sinks and the surrounding matrix. These data include all pin hits and so can exceed 100% cover. Bars not sharing letters within each data type (*Lolium* cover, *Hemizonia* cover, and percentage *Hemizonia* flowering) indicate significant differences (Tukey's HSD).

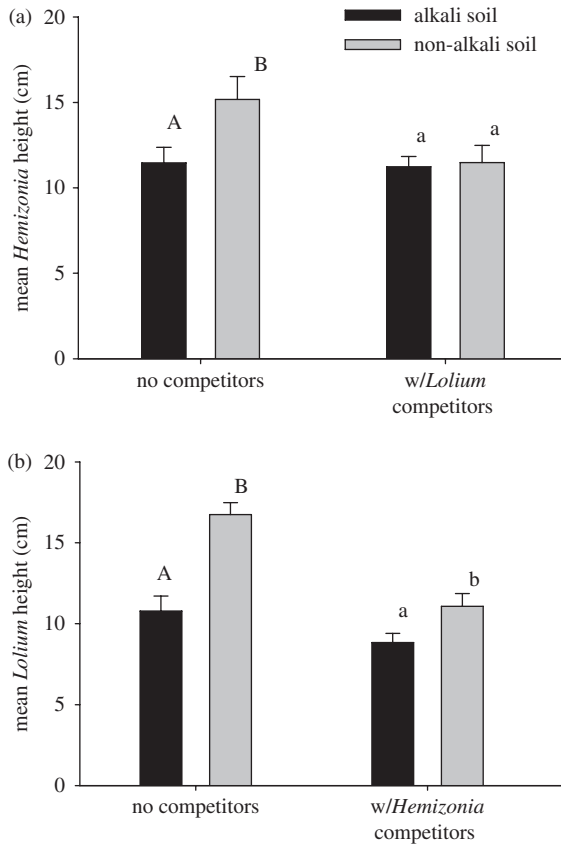
**Table 1.** Soil characteristics (mean  $\pm$  1 SE) of alkali pools and adjacent non-pool areas. Results of one-way ANOVA for each characteristic are shown in table.

	Pool (n = 4)	Non-pool (n = 4)	P
pH	8.55 $\pm$ 0.33	7.71 $\pm$ 0.16	0.04
Na (ppm)	3175 $\pm$ 428	2220 $\pm$ 362	0.14
NH <sub>4</sub> -N (ppm)	1.70 $\pm$ 0.14	1.95 $\pm$ 0.16	0.16
Water depth (cm)	4.0 $\pm$ 1.0	0.3 $\pm$ 0.1	0.006

flowering inside the pools (Fig. 1). There were no significant patterns for the other three species encountered, *Polypogon* sp. (16% cover), *Hainardia* sp. (3% cover), and *Chenopodium* sp. (3% cover), perhaps because of their rarity. Mean soil pH of pools was 8.55, significantly higher than non-pool areas, at pH 7.71, and rainy season mean water depth of pools was 4.0 cm, significantly deeper than 0.3 cm outside pools (Table 1). Alkali pools were also characterized by 43% higher sodium and 15% lower ammonium nitrogen, although these tendencies were non-significant, possibly due to low sample size (Table 1). All other soil factors tested showed no significant differences between pool and non-pool areas (all  $P > 0.60$ ).

### Greenhouse reciprocal transplant experiment

Repeated measures ANCOVA showed significant overall soil and soil  $\times$  time interaction effects (soil: *Wilk's*  $\lambda = 0.30$ ,  $F_{1,43} = 12.94$ ,  $P = 0.0008$ ; soil  $\times$  time: *Wilk's*  $\lambda = 0.13$ ,  $F_{1,43} = 5.64$ ,  $P = 0.02$ ) on *Hemizonia* height. *Hemizonia* performed better after 3 weeks on non-alkali soil, regardless of the presence or absence of *Lolium*, growing 60% taller at 3 weeks (height in alkali soil:  $0.88 \pm 0.08$  cm, non-alkali soil:  $1.41 \pm 0.12$  cm;  $F_{1,43} = 16.29$ ,  $P = 0.0002$ ). At the end of the experiment, after 6.5 weeks, *Hemizonia* continued to perform better (32% taller) on non-alkali soil, but only in the absence of competition (Fig. 2a); in the presence of competition, *Hemizonia* performance did not differ significantly between the two soil types (Fig. 2a). *Lolium* performed better in non-alkali than on alkali soil throughout the experiment. Competition did not significantly affect *Lolium* height after 3 weeks ( $F_{1,43} = 0.93$ ,  $P = 0.34$ ), but final height of *Lolium* was 28% less under competition with *Hemizonia* ( $F_{1,43} = 31.0$ ,  $P < 0.0001$ , Fig. 2b). The statistical model comparing height across species indicated that, in competition, *Lolium* performed significantly worse than *Hemizonia* in alkali soil ( $F_{1,119} = 8.84$ ,  $P = 0.004$ ), but did not differ significantly in non-alkali soil ( $F_{1,119} = 1.21$ ,  $P = 0.27$ ).



**Fig. 2.** Response of *Hemizonia* (a) and *Lolium* (b) to soil type and interspecific competition, as measured by height at the end of the experiment (6.5 weeks). Bars are 1 SE. Planned orthogonal contrasts indicate significant differences in *Hemizonia* performance between alkali and non-alkali soil in the absence of competition ( $F_{1,45} = 6.96$ ,  $P = 0.01$ ); in the presence of competition, there is no significant difference ( $F_{1,45} = 1.32$ ,  $P = 0.26$ ). For *Lolium*, performance is better in non-alkali soil than alkali soil in the presence of competition ( $F_{1,64} = 6.86$ ,  $P = 0.01$ ) and in the absence of competition ( $F_{1,64} = 38.3$ ,  $P < 0.0001$ ). Bars not sharing letters within each competition category (no competitors, with competitors) indicate significant differences.

*Hemizonia* had 57% higher germination in non-alkali soil than in alkali soil ( $F_{1,59} = 7.34$ ,  $P = 0.009$ ), although the magnitude of this difference was small (non-alkali soil:  $3.9 \pm 0.33$  seeds pot<sup>-1</sup>, alkali soil:  $2.5 \pm 0.28$ ). *Hemizonia* germination showed no other significant responses, and *Lolium* germination showed no significant responses. Results for leaf number were non-significant ( $P > 0.42$ ) for *Hemizonia*. *Lolium* consistently had more leaves on non-alkali soil ( $F_{1,64} = 19.48$ ,  $P < 0.0001$ ), with the greatest number of leaves on non-alkali soil without competitors (mean

$9.1 \pm 1.15$ ) and the least on alkali soil with competitors (mean  $3.6 \pm 0.24$ ).

## Discussion

Ecologists have long been fascinated by the mechanisms governing species distributions. Our results show that the alkali specialist, *Hemizonia pungens* ssp. *pungens*, prefers non-alkali soils to alkali soils. The results also suggest that the distribution of *Hemizonia* may be due to escaping competition from alkali-sensitive *Lolium*. The greenhouse experiments revealed that alkali soil inhibited performance of both *Lolium* and *Hemizonia*, the alkali endemic (Fig. 2). The poorer performance of *Lolium* in alkali soil was not surprising in light of *Lolium* dominance of non-alkali areas and its virtual absence from the harsh alkali areas, which have higher pH and sodium and lower nitrogen (Table 1). Despite its status as an alkali specialist, *Hemizonia* was also significantly inhibited by alkali soil conditions in the absence of competitors. This represents a rejection of our first hypothesis, that *Hemizonia* was more abundant in alkali soils because of an inherent edaphic preference for alkali conditions. These results are consistent with similar evidence from Kruckeberg (1954) for serpentine soils and Hoopes & Hall (2002) for alkali soils (see also Barbour 1970 for salt-tolerant species).

Support for the alternative (refuge) hypothesis was more tentative. *Hemizonia* preference for non-alkali soil in the absence of competition persisted throughout the experiment. In the presence of competition, however, this effect disappeared by the end of the experiment, after 6.5 weeks, when *Hemizonia* was performing just as well in alkali soil. Overall, soil type was limiting to *Hemizonia* early in its growth, while competition became increasingly important as plant size (and presumably interspecific competition) increased. This is in contrast to *Lolium*, which performed worse on alkali soil regardless of competition.

These results are suggestive of our second hypothesis (the “refuge” hypothesis), that *Hemizonia* does not actually prefer harsh alkali soil, but is simply better able to tolerate alkali soil when faced with competitors that are less tolerant of high alkali conditions. By tolerating poor soils, *Hemizonia* may achieve a refuge from competition with the less tolerant *Lolium*. This behavior is consistent with the competitor/stress tolerator dichotomy (Grime 1977) and the author’s suggestion that there is a tradeoff between competitive ability and stress tolerance,

such that a plant species will not usually be highly adapted to both stressful conditions and competitive conditions.

Affirmative evidence for the refuge hypothesis would have shown that performance of *Hemizonia* under interspecific competition was significantly worse in non-alkali soil than in alkali soil. Over the 6-week course of this experiment, all trends were in this direction. Over a longer time period, this difference may have become even more apparent. Additionally, although the height data collected in this experiment appear to give an indication of fitness, patterns were not as dramatic as would be expected from patterns in the field (e.g. dominance of *Lolium* outside of sinks). More dramatic differences may have appeared over time or with a different fitness measure, such as flowering or production of viable seeds.

Our results may also have been influenced by a gradual invasion of these harsh sites by *Lolium*. *Lolium* is a known invader of vernal pools and serpentine areas (Kruckeberg 1954; Linhart 1988), and there is evidence of ecotypic differentiation in this species (Dawson et al. 2007) and other species (Linhart 1988; Jurjavcic et al. 2002) that can result in increased tolerance to harsh areas or to competition. Some of the *Lolium* collected from inside the pools may have been an ecotype that was more adapted to competition with *Hemizonia* in alkali conditions than *Lolium* found outside the pools. We were also unable to replicate at least one of the major differences between alkali and non-alkali microsites; differences in tolerance to a second stressor – inundation in the field – may further accentuate our greenhouse patterns. Replication of this experiment in the field would better mimic natural conditions such as inundation or natural climatic variation, two important considerations when extrapolating from greenhouse results to the field. In any case, our results clearly reject the edaphic preference hypothesis and suggest a need for further testing of the edaphic refuge hypothesis as an explanation for the limited distribution of this edaphic endemic.

In other ecosystems, competition and abiotic factors are known to simultaneously influence species abundance and distribution. In a pattern similar to our results, salt marsh zonation in the south-eastern USA is partly determined by the competitive exclusion of *Spartina* from less saline sites where it is out-competed by *Juncus* (Pennings et al. 2005). The classic barnacle story from the intertidal zone is a similar example from the animal kingdom (Connell 1961). It might be tempting to suggest that these patterns are part of a more general pattern in which

competition intensity increases along productivity gradients (Grime 1973; Foster 2000; Sammul et al. 2000, but see Tilman 1988). However, a meta-analysis by Goldberg et al. (1999) found negative, but no positive, relationships between competition intensity and productivity. It is clear that competition can be important in stressful environments and that stress-tolerator species can even be superior competitors in non-stressful environments (McGraw & Chapin 1989; Emery et al. 2001). Overall, our data suggest a mechanism by which competition between native and exotic species on impoverished soils leads to dominance of native species, and refugia for native species where exotic species are unable to thrive.

**Acknowledgements.** We thank Zack Anderud, Jim Richards' lab, Kathryn Dawson, Richard Evans, Ron Lane, Leah Miller, Megan Lulow, Bob Bugg, Craig Thomsen, Jennifer Williamson Burt, Sarah Elmendorf, Michael Singer, and Kevin Rice for assistance of various kinds. J. Bakker and three anonymous reviewers provided helpful comments. Funding was provided by an NSF GRF and a UCD Jastro-Shields grant to K.E.V.

## References

- Anon. (US Fish and Wildlife Service, California Department of Fish and Game) 1996. Accessed December 2008 from [http://library.ceres.ca.gov/cgi-bin/doc\\_home?elib\\_id=1786](http://library.ceres.ca.gov/cgi-bin/doc_home?elib_id=1786)
- Anon. (CalEPPC) 1999. *Exotic Plant Pest List*. Accessed October 2004 from <http://www.ucce.ucdavis.edu/files/filelibrary/5319/4898.pdf>
- Anon. (EPS Economic and Planning Systems) 2001. *Preliminary Draft Yolo Habitat Conservation*.
- Barbour, M.G. 1970. Is any angiosperm an obligate halophyte? *American Midland Naturalist* 84: 105–129.
- Brady, K.U., Kruckeberg, A.R. & Bradshaw, H.D. 2005. Evolutionary ecology of plant adaptation to serpentine soils. *Annual Review of Ecology Evolution and Systematics* 36: 243–266.
- Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42: 710–723.
- Cremene, C., Groza, G., Rakosy, L., Schileyko, A.A., Baur, A., Erhardt, A. & Baur, B. 2005. Alterations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspots. *Conservation Biology* 19: 1606–1618.
- Danin, A. 1999. Desert rocks as plant refugia in the Near East. *Botanical Review* 65: 93–170.
- Dawson, K., Veblen, K.E. & Young, T.P. 2007. Experimental evidence for an alkali ecotype of *Lolium multiflorum*, an exotic invasive annual grass. *Biological Invasions* 9: 327–334.

- Emery, N.C., Ewanchuk, P.J. & Bertness, M.D. 2001. Competition and salt-marsh zonation: stress tolerators may be dominant competitors. *Ecology* 82: 2471–2485.
- Foster, B.L. 2000. Competition at the population level along a standing crop gradient: a field experiment in successional grassland. *Plant Ecology* 151: 171–180.
- Gerhardt, F. & Collinge, S.K. 2003. Exotic plant invasions of vernal pools in the Central Valley of California, USA. *Journal of Biogeography* 30: 1043–1052.
- Goldberg, D.E., Rajaniemi, E., Gurevitch, J. & Stewart-Oaten, A. 1999. Empirical approaches to quantifying interaction intensity: competition along productivity gradients. *Ecology* 80: 1118–1131.
- Gram, W.K., Borer, E.T., Cottingham, K.L., Seabloom, E.W., Boucher, V.L., Goldwasser, L., Micheli, F., Kendall, B.E. & Burton, R.S. 2004. Distribution of plants in a California serpentine grassland: are rocky hummocks spatial refuges for native species? *Plant Ecology* 172: 159–171.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344–347.
- Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111: 1169–1194.
- Hannaway, D., Fransen, S., Cropper, J., Teel, M., Chaney, M., Griggs, T., Halse, R., Hart, J., Cheeke, P., Hansen, D., Klinger, R. & Lane, W. 1999. Annual ryegrass (*Lolium multiflorum* Per.). Accessed 5 December 2005 from <http://www.eesc.orst.edu/agcomwebfile/edmat/html/pnw/pnw501/intro.html>.
- Harrison, S., Grace, J.B., Davies, K.F., Safford, H.D. & Viers, J.H. 2006. Invasion in a diversity hotspot: exotic cover and native richness in the Californian serpentine flora. *Ecology* 87: 695–703.
- Hart, R. 1980. The coexistence of weeds and restricted native plants on serpentine barrens in Southeastern Pennsylvania. *Ecology* 61: 688–701.
- Hickman, J.C. 1993. *The Jepson manual of higher plants of California*. University of California Press, Berkeley, CA, US.
- Hoopes, M. & Hall, L. 2002. Edaphic factors and competition affect pattern formation and invasion in a California grassland. *Ecological Applications* 12: 24–39.
- Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A. & Vitousek, P.M. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71: 478–491.
- Jurjavic, N.L., Harrison, S. & Wolf, A.T. 2002. Abiotic stress, competition, and the distribution of the native grass *Vulpia microstachys* in a mosaic environment. *Oecologia* 130: 555–562.
- Kruckeberg, A.R. 1954. The ecology of serpentine soils. 3. Plant species in relation to serpentine soils. *Ecology* 35: 267–274.
- Liancourt, P., Callaway, R.M. & Michalet, R. 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* 86: 1611–1618.
- Linhart, Y.B. 1988. Intrapopulation differentiation in annual plants. III. The contrasting effects of intra- and interspecific competition. *Evolution* 42: 1047–1064.
- McGraw, J.B. & Chapin, F.S. III 1989. Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. *Ecology* 70: 736–749.
- Pennings, S.C., Grant, M.B. & Bertness, M.D. 2005. Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. *Journal of Ecology* 93: 159–167.
- Pugnaire, F.I. & Luque, M.T. 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93: 42–49.
- Sammul, M., Kull, K., Oksanen, L. & Veromann, P. 2000. Competition intensity and its importance: results of field experiments with *Anthoxanthum odoratum*. *Oecologia* 125: 18–25.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, NJ, US.
- Tiner, R.W. 2003. Geographically isolated wetlands of the United States. *Wetlands* 23: 494–516.
- Williamson, J. & Harrison, S. 2002. Biotic and abiotic limits to the spread of exotic revegetation species. *Ecological Applications* 12: 40–51.
- Wilson, S.D. & Keddy, P.A. 1986. Species competitive ability and position along a natural stress/disturbance gradient. *Ecology* 67: 1236–1242.
- Wright, J.W., Stanton, M.L. & Scherson, R. 2006. Local adaptation to serpentine and non-serpentine soils in *Collinsia sparsiflora*. *Evolutionary Ecology Research* 8: 1–21.
- Xu, Z.R. 1995. A study of the vegetation and floristic affinity of the limestone forests in Southern and Southwestern China. *Annals of the Missouri Botanical Garden* 82: 570–580.
- Zedler, P.H. 2003. Vernal pools and the concept of “isolated wetlands”. *Wetlands* 23: 597–607.

Received 26 October 2007;

Accepted 9 April 2008.

Co-ordinating Editor: Jan P. Bakker