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

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13 **Key words**

14 abiotic; alkali sinks; context-dependent competition; edaphic mosaic; refuge hypothesis;

15 ryegrass; tar plant

16

17 **Abstract**

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

23 Location: Central Valley, California, USA

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

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

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

37 and refugia of native species where exotic species are unable to thrive.

38

39 **Introduction**

40 One of the primary goals of ecology is determining the factors that affect the distribution and
41 abundance of species. Distributions of plant populations are limited by a combination of biotic
42 factors, such as competition, and abiotic factors, such as edaphic conditions. Understanding the
43 relative contributions of these limiting factors is especially interesting when considering
44 observed patterns of “edaphic endemism.”

45 Edaphically severe habitats commonly support edaphic endemics, specialized plant
46 species that do not occur elsewhere. Examples of edaphic endemism include serpentine outcrops
47 (Brady et al. 2005, Gram et al. 2004, Harrison et al. 2006), limestone and calcareous soils
48 (Cremene et al. 2005, Danin 1999, Xu 1995), vernal pools (Gerhardt & Collinge 2003, Zedler
49 2003) and desert springs (Tiner 2003). These habitats tend to exist as isolated populations
50 patchily distributed on the landscape, with the potential to greatly contribute to both local and
51 regional diversity.

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

59 The endemism of specialized plant species in edaphically severe sites suggests either a)

60 that edaphic endemics are so specialized for growth under the conditions prevalent in these areas
61 that they perform inherently better than on more moderate soil conditions, or b) that these areas
62 represent refuges from competition with other plant species (Hoopes & Hall 2002, Williamson &
63 Harrison 2002), which in California grasslands are often exotic annual grasses. Evidence from
64 other ecosystems suggests that, for some species, stressful environments may serve as refuges
65 from competition (Liancourt et al. 2005, Pugnaire & Luque 2001, Wilson & Keddy 1986). Over
66 50 years ago, Kruckeberg (1954) hypothesized that the restriction of serpentine endemics was
67 not due to an inherent preference of these species for the severe edaphic conditions on serpentine
68 soils, but rather that "serpentine endemics are able to maintain themselves in open serpentine
69 communities where competition is not severe, but not in the more rigorous competition of non-
70 serpentine soils" (Kruckeberg 1954, p.272). He then provided experimental evidence that this
71 was indeed the case. Since then there have been few experimental examinations of these patterns
72 and no formal tests of the refuge hypothesis. Jurjavcic et al. (2002) found conflicting
73 experimental patterns of competition and tolerance on serpentine soils in *Vulpia microstachys*,
74 which is not a serpentine specialist. Hart (1980) found results suggestive of a refuge effect in
75 serpentine outcrops, but did not directly test this effect. In the context of alkali sinks and alkali
76 endemics, Hoopes and Hall (2002) presented experimental evidence merely suggestive of the
77 refuge effect in *Sporobolus airoides* (alkali sacaton). In contrast, Wright et al. (2006) present
78 evidence from a reciprocal transplant experiment that the serpentine ecotype of *Collinsia*
79 *sparsiflora* did indeed perform better on serpentine soils than on non-serpentine soils, even in the
80 absence of competition. Therefore both the refuge hypothesis and the edaphic preference
81 hypotheses remain viable alternatives for explaining edaphic endemism, and the answers may
82 well be species- and site-specific. Here we present evidence from an experimental test of the

83 hypothesis that the restriction of individuals of the alkali endemic *Hemizonia pungens* ssp.
84 *pungens* (Hook and Arn.) Torr. and Gray is not due to a preference for strongly alkali soils, but
85 rather to the refuge from competition provided by these soils.

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

93

94 **Methods**

95 *Study site and focal species*

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

101 Our study area was a seasonally inundated pasture with scattered alkali sinks (25—
102 200m²) located in Yolo County, CA (38° 37' N, 121° 43' W) approximately 10km northwest of
103 Davis, now part of the Alkali Grasslands Reserve. These sinks are part of a series of alkali sinks
104 in this area appearing to be of geologic origin (M. Singer, pers. comm.), and they host a number
105 of rare and endemic alkali specialists (EPS 2001). In our study area, the native alkali specialist,

106 *Hemizonia pungens pungens* dominates these sinks, with the surrounding matrix dominated by
107 the invasive exotic *Lolium multiflorum*.

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

119

120 *Soil and vegetation surveys*

121 In May 2005, we surveyed four alkali pools off Road 25 in Yolo County, California. There was
122 no longer standing water in the pools at the time of the survey, but the plants were still fully
123 green. Pools were identified by local topography, *Hemizonia* dominance, and (salt-encrusted)
124 bare ground, while non-pools were areas of dense *Lolium* monoculture. At each of four pools,
125 we placed three 1m x 1m quadrats in each of three microsites: pool, edge and background (non-
126 pool), for a total of 36 quadrats. In each quadrat we placed a ten-point pin frame, and counted
127 total hits by each plant species. We also estimated the percent of *Hemizonia* plants that were
128 flowering. At each pool and background microsite, we collected one soil sample from 0-10cm

129 (eight soil samples total), and air-dried them. We measured pH of these samples in the lab with a
130 1:1 ratio of soil and deionized water. The UC Davis DANR soils laboratory analyzed the soil
131 samples for total sodium, ammonium nitrogen, nitrate nitrogen, potassium, calcium and
132 magnesium. Pools were surveyed for maximum water depth at the height of the rainy season in
133 February 2006.

134

135 *Greenhouse reciprocal transplant experiment*

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

144 During May and June, 2003, we collected *Hemizonia* seeds from randomly selected
145 plants growing inside the alkali sinks and *Lolium* from plants growing inside and outside the
146 sinks. Seeds were stored in envelopes at room temperature for seven months. Based on results
147 of earlier germination trials, we soaked *Hemizonia* seeds in 10% bleach solution for five minutes,
148 then in deionized water for five minutes. We then stratified the seeds for 18 days by placing
149 them between wet paper towels in plastic bags stored at 10° C. *Lolium* seeds were similarly
150 soaked in bleach solution and deionized water, but did not need stratification. In April 2004 we
151 seeded *Hemizonia* at a rate of 25 seeds per pot, and *Lolium* one week later (to synchronize

152 seedling emergence) at a rate of 10 seeds per pot.

153 Sixty pots were arranged on a greenhouse mist bench at UC Davis in a full-factorial
154 randomized complete block design. In each of ten blocks, we crossed two levels of competition
155 (interspecific competitor present vs. absent) with two soil types (alkali soil vs. non-alkali), for
156 each species. By “non-alkali” here (and throughout), we mean the considerably less alkali soils
157 in the grassland matrix, which were still slightly basic. Plant-soil treatment combinations were:
158 1) *Hemizonia* only, alkali soil, 2) *Hemizonia* only, non-alkali soil, 3) *Lolium* only, alkali soil, 4)
159 *Lolium* only, non-alkali soil, 5) *Hemizonia+Lolium*, alkali soil, 6) *Hemizonia+Lolium*, non-alkali
160 soil.

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

174 *Statistical analyses*

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

179 We used repeated measures ANCOVA to assess the effects of interspecific competition
180 and soil type on greenhouse seedlings at three weeks and 6.5 weeks. For each response variable
181 for each plant species, we included block, soil type (alkali vs. non-alkali), interspecific
182 competition (presence vs. absence), and soil type*interspecific competition as factors in our
183 model. Number of competitors (ranging from one to five) was treated as a covariate. Response
184 variables for both *Lolium* and *Hemizonia* were height at three weeks and 6.5 weeks. To test our
185 two hypotheses, class means were compared with planned independent orthogonal contrasts.
186 This statistical model was used to test number of leaves and germination percentage as well,
187 though germination excluded number of competitors as the covariate. Although we do not know
188 whether height provides a reliable estimate of relative performance across species, we performed
189 an additional analysis to compare final height of both species; model effects were focal species
190 (*Hemizonia* vs. *Lolium*), soil, competition, soil * competition interaction, and number of
191 competitors as the covariate. Independent contrasts were used to test our hypotheses that
192 *Hemizonia* out-competed *Lolium* in alkali soil, and vice-versa on non-alkali soil.

193

194 **Results**

195 *Soil and vegetation surveys*

196 Our vegetation sampling quantified the differences in species' abundances and performance
197 between pool and non-pool sites. *Hemizonia* abundance was five times higher inside pools than

198 in the surrounding matrix ($P < .05$), and *Lolium* was abundant in the matrix, but rare in the pools
199 ($P < 0.05$, Figure 1). The few *Hemizonia* individuals outside the pools rarely flowered,
200 compared to nearly 100% flowering inside the pools (Figure 1). There were no significant
201 patterns for the other three species encountered, *Polypogon* sp. (16% cover), *Hainardia* sp. (3%
202 cover), and *Chenopodium* sp. (3% cover), perhaps because of their rarity. Mean soil pH of
203 pools was 8.55, significantly higher than non-pool areas of pH 7.71, and rainy season mean
204 water depth of pools was 4.0 cm, significantly deeper than 0.3 cm outside (Table 1). Alkali
205 pools also were characterized by 43% higher sodium and 15% lower ammonium nitrogen,
206 though these tendencies were non-significant, possibly due to low sample size (Table 1). All
207 other soil factors tested showed no significant differences between pool and non-pool areas (all P
208 > 0.60).

209

210 *Greenhouse reciprocal transplant experiment*

211 Repeated measures ANCOVA showed significant overall soil and soil * time interaction effects
212 (soil: *Wilk's* $\lambda = 0.30$, $F_{1,43}=12.94$, $P = .0008$; soil*time: *Wilk's* $\lambda = 0.13$, $F_{1,43} = 5.64$, $P = .02$) on
213 *Hemizonia* height. *Hemizonia* performed better after three weeks on non-alkali soil, regardless
214 of the presence or absence of *Lolium*, growing 60% taller at three weeks (height in alkali soil:
215 0.88 ± 0.08 cm, non-alkali soil: 1.41 ± 0.12 cm; $F_{1,43}=16.29$, $P = 0.0002$). At the end of the
216 experiment, after 6.5 weeks, *Hemizonia* continued to perform better (32% taller) on non-alkali
217 soil, but only in the absence of competition (Figure 2a); in the presence of competition,
218 *Hemizonia* performance did not differ significantly between the two soil types (Figure 2a).
219 *Lolium* performed better in non-alkali soil than on alkali soil throughout the experiment.
220 Competition did not significantly affect *Lolium* height after three weeks ($F_{1,43}=93$, $P = 0.34$), but

221 final height of *Lolium* was 28% less under competition with *Hemizonia* ($F_{1,43}= 31.0, P <.0001$,
222 Figure 2b). The statistical model comparing height across species indicated that, in competition,
223 *Lolium* performed significantly worse than *Hemizonia* in alkali soil ($F_{1,119}= 8.84, P = 0.004$), but
224 did not differ significantly in non-alkali soil ($F_{1,119}= 1.21, P = 0.27$).

225 *Hemizonia* had 57% greater germination in non-alkali soil than in alkali soil ($F_{1,59}=7.34$,
226 $P = 0.009$), though the magnitude of this difference was small (non-alkali soil: 3.9 ± 0.33 seeds
227 per pot, alkali soil: 2.5 ± 0.28). *Hemizonia* germination showed no other significant responses,
228 and *Lolium* germination showed no significant responses. Results for leaf number were non-
229 significant ($P > 0.42$) for *Hemizonia*. *Lolium* consistently had more leaves on non-alkali soil
230 ($F_{1,64}=19.48, P <.0001$), with the greatest number of leaves on non-alkali soil without
231 competitors (mean 9.1 ± 1.15) and the least on alkali soil with competitors (mean 3.6 ± 0.24).

232

233 **Discussion**

234 Ecologists have long been fascinated by the mechanisms governing species distributions.
235 Our results show that the alkali specialist, *Hemizonia pungens* ssp. *pungens*, prefers non-alkali
236 soils to alkali soils. Our results also suggest that the distribution of *Hemizonia* may be due to
237 escaping competition from alkali-sensitive *Lolium*. Our greenhouse experiments revealed that
238 alkali soil inhibited performance of both *Lolium multiflorum* and *Hemizonia*, the alkali endemic
239 (Figure 2). The poorer performance of *Lolium* in alkali soil was not surprising in light of *Lolium*
240 dominance of non-alkali areas and its virtual absence from the harsh alkali areas, with their
241 higher pH and sodium and lower nitrogen (Table 1). Despite its status as an alkali specialist,
242 *Hemizonia* was also significantly inhibited by alkali soil conditions in the absence of
243 competitors. This represents a rejection of our first hypothesis: that *Hemizonia* was more

244 abundant in alkali soils because of an inherent edaphic preference for alkali conditions. These
245 results are consistent with similar evidence from Kruckeberg (1954) from serpentine soils and
246 Hoopes and Hall (2002) from alkali soils (see also Barbour 1970 for salt-tolerant species).

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

254 These results are suggestive of our second hypothesis (the “refuge” hypothesis): that
255 *Hemizonia* does not actually prefer harsh alkali soil, but is simply better able to tolerate alkali
256 soil when faced with competitors that are less tolerant of high alkali conditions. By tolerating
257 poor soils, *Hemizonia* may achieve a refuge from competition with the less tolerant *Lolium*. This
258 behavior would be consistent with the competitor/stress tolerator dichotomy (Grime 1977) and
259 his suggestion that there is a tradeoff between competitive ability and stress tolerance such that a
260 plant species will not usually be highly adapted to both stressful conditions and competitive
261 conditions.

262 Affirmative evidence for the refuge hypothesis would have shown that performance of
263 *Hemizonia* under interspecific competition was significantly worse in non-alkali soil than in
264 alkali soil. Over the six-week course of this experiment, all trends were in this direction. Over a
265 longer time period, this difference may have become even more apparent. Additionally, although
266 the height data collected in this experiment appear to give an indication of fitness, patterns were

267 nowhere as dramatic as would be expected from patterns in the field (e.g., dominance of *Lolium*
268 outside of sinks). More dramatic differences may have appeared over time or with a different
269 fitness measure, such as flowering or production of viable seeds.

270 Our results also may have been influenced by a gradual invasion of these harsh sites by
271 *Lolium*. *Lolium* is a known invader of vernal pools and serpentine areas (Kruckeberg 1954,
272 Linhart 1988), and there is evidence that ecotypic differentiation in this species (Dawson et al.
273 2007) and other species (Jurjavcic et al. 2002, Linhart 1988) can result in increased tolerance to
274 harsh areas or to competition. Some of the *Lolium* that was collected from inside the pools may
275 have been an ecotype more adapted to competition with *Hemizonia* in alkali conditions than
276 *Lolium* found outside the pools. We also were unable to replicate at least one of the major
277 differences between alkali and non-alkali microsites; differences in tolerance to a second
278 stressor-- inundation in the field-- may further accentuate our greenhouse patterns. Replication of
279 this experiment in the field would better mimic field natural conditions such as inundation or
280 natural climatic variation, two important considerations when extrapolating from greenhouse
281 results to the field. In any case, our results clearly reject the edaphic preference hypothesis and
282 suggest a need for further testing of the edaphic refuge hypothesis as an explanation for the
283 limited distribution of this edaphic endemic.

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

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

298

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305

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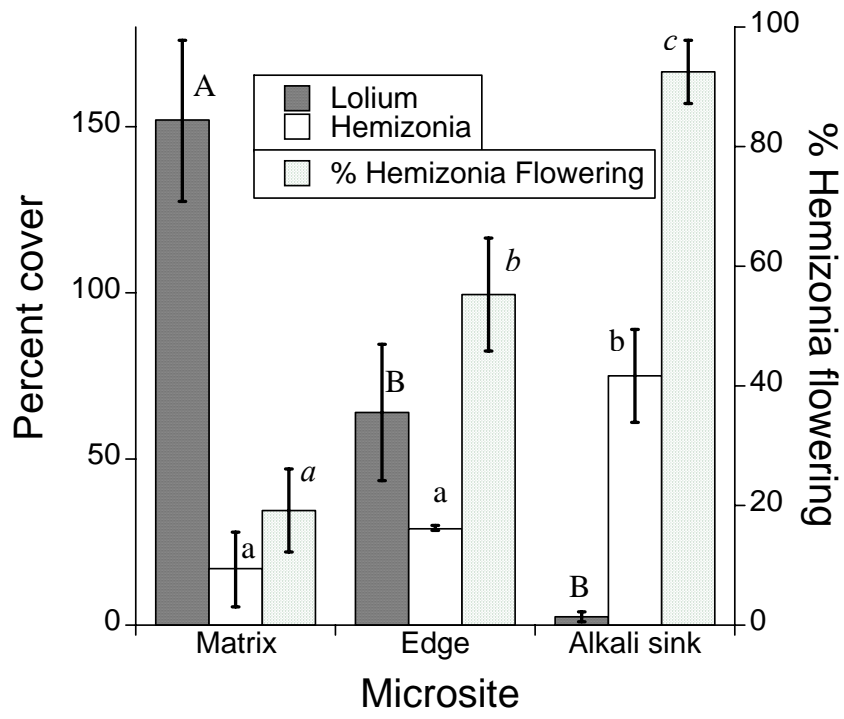
390 **Figure legends**

391 Figure 1. Quantification of the visual differences between alkali sinks and the surrounding
392 matrix. These data include all pin hits and so can exceed 100% cover. Bars not sharing letters
393 within each data type (*Lolium* cover, *Hemizonia* cover and % *Hemizonia* flowering) indicate
394 significant differences (Tukeys HSD).

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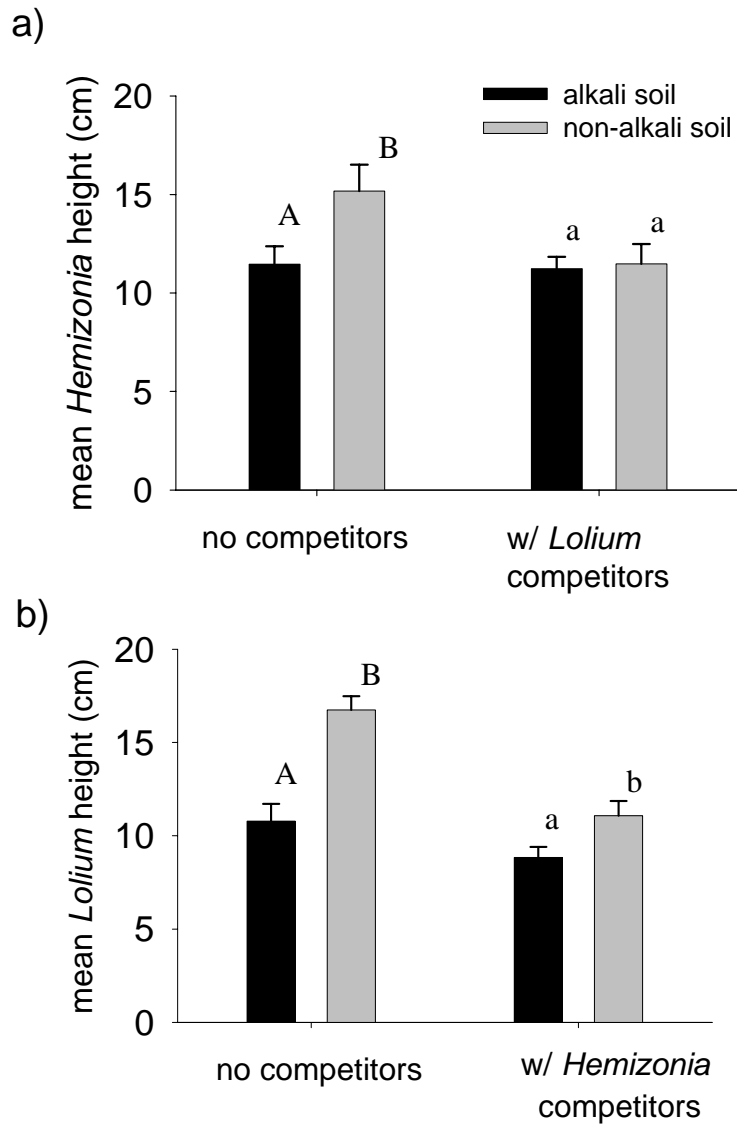
396 Figure 2. Response of *Hemizonia* (a) and *Lolium* (b) to soil type and interspecific competition,
397 as measured by height at the end of the experiment (6.5 weeks). Bars are one standard error.
398 Planned orthogonal contrasts indicate significant differences in *Hemizonia* performance between
399 alkali and non-alkali soil in the absence of competition ($F_{1,45} = 6.96, P = 0.01$); in the presence of
400 competition, there is no significant difference ($F_{1,45} = 1.32, P = 0.26$). For *Lolium*, performance is
401 better in non-alkali soil than alkali soil in the presence of competition ($F_{1,64} = 6.86, P = 0.01$) and
402 in the absence of competition ($F_{1,64} = 38.3, P < .0001$). Bars not sharing letters within each
403 competition category (no competitors, with competitors) indicate significant differences.

404 **Figure 1.**
405



406

407 **Figure 2.**
408



409

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

412

	Pool (n=4)	Non-pool (n=4)	<i>P</i>
pH	8.55 \pm 0.33	7.71 \pm 0.16	0.04
Na (ppm)	3175 \pm 428	2220 \pm 362	0.14
NH₄-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

413