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California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence

Joel K. Abraham^{1*}, Jeffrey D. Corbin^{1,2}, and Carla M. D'Antonio^{1,3}

¹*University of California, Berkeley, Department of Integrative Biology, Berkeley, CA 94720-3140, USA.*

²*Present Address: Union College, Department of Biological Sciences, Schenectady, NY 12308, USA.*

³*Present Address: University of California, Santa Barbara, Ecology, Evolution & Marine Biology, Santa Barbara, CA 93106, USA.*

*Author for correspondence: (email: jabraham@berkeley.edu; phone: +1-510-643-5782)

46 **Keywords**

47 *Exotic species, fertilization, germination, invasion, priority effects, seedling dynamics*
48

49 **Abstract**

50 Early emergence of plant seedlings can offer strong competitive advantages over
51 later-germinating neighbors through the preemption of limiting resources. This
52 phenomenon may have contributed to the persistent dominance of European annual
53 grasses over native perennial grasses in California grasslands, since the former
54 species typically germinate earlier in the growing season than the latter and grow
55 rapidly after establishing. Recently, European perennial grasses have been spreading
56 into both non-native annual and native perennial coastal grass stands in California.
57 These exotic perennials appear to be less affected by the priority effects arising from
58 earlier germination by European annual grasses. In addition, these species
59 interactions in California grasslands may be mediated by increasing anthropogenic or
60 natural soil nitrogen inputs. We conducted a greenhouse experiment to test the effects
61 of order of emergence and annual grass seedling density on native and exotic
62 perennial grass seedling performance across different levels of nitrogen availability.
63 We manipulated the order of emergence and density of an exotic annual grass
64 (*Bromus diandrus*) grown with either *Nassella pulchra* (a native perennial grass),
65 *Festuca rubra* (native perennial) or *Holcus lanatus* (exotic perennial), with and
66 without added nitrogen. Earlier *B. diandrus* emergence and higher *B. diandrus*
67 density resulted in greater reduction in the aboveground productivity of the perennial
68 grasses. However, *B. diandrus* suppressed both native perennials to a greater extent
69 than it did *H. lanatus*. Nitrogen addition had no effect on the productivity of native
70 perennials, but greatly increased growth of the exotic perennial *H. lanatus*, grown
71 with *B. diandrus*. These results suggest that the order of emergence of exotic annual
72 versus native perennial grass seedlings could play an important role in the continued
73 dominance of exotic annual grasses in California. The expansion of the exotic
74 perennial grass *H. lanatus* in coastal California may be linked to its higher tolerance
75 of earlier-emerging annual grasses and its ability to access soil resources amidst high
76 densities of annual grasses.

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84 **Introduction**

85 The order of emergence among competitors affects the growth, survival, and
86 fecundity of plants across a wide range of species, especially in situations with well-
87 defined growth windows and high densities of competitors (Miller et al. 1994; Verdù
88 and Traveset 2005). Early emergence in relation to competitors can allow for
89 preemption of available resources by the early emerging species, yielding
90 disproportionate advantages (Ross and Harper 1972). Once established, the early-
91 emerging species may maintain dominance even if it is a relatively poor competitor
92 during later life-stages.

93 Priority effects have been well documented in grasses (Harper 1961; Ross and
94 Harper 1972; Miller 1987; D'Antonio et al. 2001), and may be of particular
95 importance in maintaining the current structure of California grasslands. These
96 grasslands have experienced extensive invasion by exotic annual grasses and steep
97 declines in native perennial bunchgrasses over the last two centuries (Heady 1988;
98 D'Antonio et al. 2007). The continued success of exotic annual grasses suggests some
99 competitive advantage over native perennial grasses (Dyer and Rice 1997; Hamilton
100 et al. 1999; Corbin et al. 2007), although the two groups coexist in some coastal
101 prairie sites (Heady *et al.* 1988; Stromberg et al. 2001). Several studies have shown
102 that mature native perennial grasses can successfully compete with exotic annuals
103 (e.g. Peart 1989b; Seabloom et al. 2003; Corbin and D'Antonio 2004b; Lulow 2006),
104 but the natives may be sensitive to competition with annual plants at the seedling
105 stage particularly because exotic annual grasses tend to emerge at much higher
106 densities and earlier than native perennial grasses (Dyer and Rice 1997; Hamilton et
107 al. 1999; Humphrey and Schupp 2004; DiVittorio et al. 2007). Exotic annual grasses
108 germinate days after the first fall or winter rains while native perennial grasses are
109 typically slower to germinate (e.g. Reynolds et al. 2001). Subsequent aboveground

110 production of exotic annual grasses outpaces that of native perennial grasses,
111 potentially reducing light, water, and nutrients available for emerging perennial
112 seedlings (Jackson and Roy 1986; Dyer and Rice 1999). While some native
113 bunchgrass adults are thought to be long-lived (Hamilton et al. 1999), they can
114 eventually succumb to drought, burrowing animals or other mortality sources. If they
115 cannot successfully recruit due to seedling competition from exotic annual grasses,
116 then populations should eventually decline.

117 Efforts to reintroduce native perennial bunchgrasses have had limited success
118 when annuals are present at their typical high densities (Wilson and Gerry 1995; Dyer
119 and Rice 1999; Clausnitzer et al. 1999; Brown and Rice 2000). Management
120 strategies that negate priority effects and reduce the strength of annual grass
121 competition via reduced performance or density should improve the survival of
122 perennial grass seedlings and increase the success of restoration efforts (Corbin et al.
123 2004). For example, supplementing native seed supply (Seabloom et al. 2003),
124 killing annual grasses or their seeds (Stromberg and Kephart 1996; Moyes et al.
125 2005), or the planting of native perennial grasses as seedling plugs rather than seeds
126 (Dyer et al. 1996; Buisson et al. 2006) increases native grass establishment in
127 restoration sites, demonstrating the strong role exotic annual seedling density plays in
128 the suppression of native perennial grass establishment.

129 Beyond the competitive advantage gained by exotic annual grasses via earlier
130 and abundant germination, grassland restoration efforts in California also need to deal
131 with large increases in soil nitrogen availability due to atmospheric nitrogen
132 deposition and colonization by nitrogen-fixing shrubs (Maron and Connors 1996;
133 Vitousek et al. 1997; Weiss 1999, 2006; Fenn et al. 2003; Haubensak et al. 2004; Dise
134 and Stevens 2005). Increases in soil nitrogen availability are hypothesized to confer a
135 competitive advantage to fast-growing exotic species (Vitousek et al. 1987; Huenneke

136 et al. 1990; Burke and Grime 1996), and appear to disproportionately benefit exotic
137 annual grasses in California (e.g. Huenneke et al. 1990; Maron and Connors 1996;
138 Kolb et al. 2002; Lowe et al. 2003). For example, encroachment by non-native
139 annual grasses onto serpentine-derived soils, long a refuge from exotic annual grass
140 competition for many California native grassland species, occur when soil nitrogen
141 levels become elevated (Huenneke et al. 1990; Weiss 1999). Continued increases in
142 nitrogen deposition predicted through the next century (Phoenix et al. 2006; Weiss
143 2006) could have widespread consequences for patterns of exotic species invasion
144 and spread. Restoration strategies in California coastal grasslands will need to
145 include the direct and indirect effects of soil nitrogen enrichment on native perennial
146 grass versus exotic annual grass performance.

147 Even as restoration efforts to reestablish native perennial grasses continue,
148 exotic perennial grasses such as *Holcus lanatus*, *Festuca arundinaceae*, and *Phalaris*
149 *aquatica* have begun a second transformation of some areas in western grasslands
150 (Elliott and Wehausen 1974; Foin and Hektner 1986; Peart 1989a; Ewing 2002). The
151 ability of exotic perennial grasses to colonize the same annual-dominated stands that
152 have excluded native perennial reestablishment (Foin and Hektner 1986; Peart 1989c)
153 suggests that at least some European perennial grass species are less susceptible to
154 priority effects and competition from annual grasses. Given the shared life-history of
155 California and European perennial bunchgrasses, the differential success of exotic
156 versus native perennials may be linked to subtle differences in reproductive output,
157 germination timing or seedling growth traits, or responses to soil nitrogen enrichment.
158 For example, *Holcus lanatus*, a common exotic perennial invader in mesic coastal
159 grassland, produces copious seed (Peart 1989a), has higher relative growth rates than
160 some California native perennial grass species (Thomsen et al. 2006a; Corbin and
161 D'Antonio unpublished data), and appears to be highly responsive to nitrogen

162 enrichment (Schippers et al. 1999; Thomsen et al. 2006a). This species may thus be
163 less hindered than native perennial grasses by rapidly germinating exotic annuals or
164 high soil nitrogen availability at the seedling stage. Comparisons of the performance
165 of native vs. exotic perennial grass seedlings when faced with soil nitrogen
166 enrichment or competition with exotic annual grasses may help explain the disparity
167 in their ability to colonize annual dominated grasslands.

168 Our objective in this study was to determine the importance of annual grass
169 emergence time and density to the growth of native and exotic perennial grass
170 seedlings with and without nitrogen addition. We hypothesized that:

- 171 1) Reversing the typical “annual-followed-by-perennial grass” order of
172 emergence should increase perennial (native and exotic) grass seedling growth
173 by negating the priority effect.
- 174 2) Performance of the native perennial grass seedlings should be reduced to a
175 greater extent than performance of exotic perennial grass seedlings when
176 grown with high densities of exotic annual grasses.
- 177 3) The negative impact of exotic annual grasses on native perennial grasses
178 should be greater with added nitrogen because of the greater ability of annuals
179 to respond rapidly to increased resource availability. By contrast, N addition
180 should either have no effect or benefit exotic perennials grown with exotic
181 annuals.

182 We tested these hypotheses in a greenhouse using grass seedlings grown from
183 seed. We experimentally manipulated annual grass emergence time, annual grass
184 density, and soil nitrogen availability and tracked performance of native and non-
185 native perennial grasses.

186

187 **Materials and Methods**

188 **Study Species and Source Population Description**

189 We chose *Nassella pulchra* A. Hitchcock (Barkworth), *Festuca rubra* L., and *Holcus*
190 *lanatus* L. as the target perennial species, and *Bromus diandrus* Roth as the annual
191 competitor. Henceforward, the grasses will be referred to by their generic names; all
192 nomenclature follows Hickman (1993). These grass species co-occur in their ranges
193 in California (Hickman 1993). *Nassella* is a native perennial grass that was
194 historically abundant throughout California (Heady 1988), is among the most
195 common native bunchgrasses today in the California Floristic Province (Bartolome
196 and Gemmill 1981), and is a widely used species in grassland restoration. *Festuca* is
197 a coastally restricted species that remains abundant in some remnant prairies
198 (Stromberg et al. 2001). *Holcus* is an exotic perennial invader in mesic coastal and
199 inland California grasslands, encroaching on both non-native annual dominated and
200 remnant native perennial patches (Peart 1989a; Corbin et al. 2007). *Bromus* is a
201 widespread Eurasian species that appears to be a strong competitor in California
202 annual grasslands (Wilken and Painter 1993), particularly in more nitrogen-rich sites
203 (Maron and Jefferies 1999; Rice and Nagy 2000; Hoopes and Hall 2002).

204 We collected seeds of all of the species at Tom's Point Preserve (38°13'N,
205 122°57'W), a private nature reserve near Tomales, CA, USA. The site has been the
206 location for a number of field studies focused on competition and resource use of
207 native perennial, exotic perennial, and exotic annual grasses (e.g. Corbin and
208 D'Antonio 2004a,b; Corbin et al. 2005; DiVittorio et al. 2007). The vegetation is a
209 mosaic of exotic annual, native perennial or exotic perennial species with large
210 patches of *Holcus* and *Bromus*.

211

212 **Experimental Design**

213 We conducted the experiment in the Oxford Tract Greenhouse at the University of
214 California, Berkeley from March 8, 2002 to June 4, 2002 under ambient temperature
215 conditions. We arranged the experiment in a randomized full factorial design, with
216 the following fixed factors: focal perennial species (*Nassella*, *Festuca*, *Holcus*),
217 *Bromus* density (low, high), nitrogen availability (low, high), and *Bromus* emergence
218 time (simultaneous, delayed). All pots were mixed species in that they had *Bromus*
219 with three individuals of one of the perennial grass species. In addition to the mixed
220 species pots, we planted perennial grasses in monoculture (three individuals) and
221 crossed the monoculture treatments with nitrogen availability to measure perennial
222 grass response without interspecific competitors. The monoculture pots with ambient
223 nitrogen treatment for each perennial species served as a baseline of growth for that
224 species (see below). We replicated each treatment eight times.

225 Using a 50% fine sand, 50% peat moss soil mix (UC mix) we planted seeds of
226 a given focal species (*Nassella*, *Festuca* or *Holcus*) in each perennial treatment pot
227 (10 L, 20 cm diameter). After emergence, we thinned the germinated plants in each
228 pot to three seedlings spaced a minimum of 5 cm from each other and the side of the
229 pot. We transplanted additional seedlings to pots with fewer than three emerged
230 perennials.

231 We planted *Bromus* seeds either concurrently with the planting of the
232 perennial seeds (“simultaneous”) or 14 days afterwards (“delayed”). This design
233 allowed us to evaluate how variation in early seedling growth timing interacts with
234 exotic annual density and identity of the competitor (perennial species).

235 We planted *Bromus* at two densities: “high” (1592 seeds m⁻², 50 seeds/pot)
236 and “low” (637 seeds m⁻², 20 seeds/pot). We based our high-density treatment on the
237 density of annual seeds found in an equivalent area of *Bromus* dominated stands at

238 Tom's Point preserve (DiVittorio et al. unpublished data) and elsewhere in the state
239 (Young et al. 1981). The low-density treatment was meant to approximate annual
240 grass seed densities reduced by management, but is not based on field measurements.

241 To create the "high" soil nitrogen treatment, we added 0.93 g of blood meal
242 (Green All 100% Organic Blood Meal; 13-0-0) to the wet soil surface in three doses
243 (0, 30, 60 days after perennial planting). This "high" level of nitrogen addition (10 g
244 N m⁻² over the course of the experiment) is consistent with estimates of soil nitrogen
245 input by nitrogen fixing shrubs in some coastal grasslands (Maron and Jefferies 1999;
246 Haubensak et al. 2004) and falls within the range of nitrogen fertilization used in
247 previous grassland studies (e.g. Inouye and Tilman 1988). No nitrogen was added to
248 the "low" soil nitrogen treatment.

249 We positioned pots randomly with respect to treatment in the greenhouse, and
250 rotated within and between benches every two weeks. We watered plants to soil
251 saturation three or four times per week. At the first appearance of a developing
252 *Bromus* flowering culm, we destructively sampled all plants by cutting at the soil
253 surface and separated material by species. After drying the aboveground plant
254 material in an oven at 70°C for two days, we recorded the mean individual dry
255 biomass of each species by pot.

256

257 **Statistical Analysis**

258 We converted biomass measurements into an index of relative shoot yield per plant
259 (RYP), calculated as the perennial biomass in an experimental treatment divided by
260 the mean biomass of the conspecific monoculture treatment plants in ambient
261 nitrogen (hereafter referred to as control): $RYP = \text{Biomass}_{\text{experimental}} / \text{Mean}$
262 $\text{Biomass}_{\text{control}}$. This index allowed us to compare across the perennial grasses in

263 evaluating the relative effect of the treatments on their growth (Johansson and Keddy
264 1991).

265 We performed all statistical tests with SYSTAT 11.0 (Systat Software, Inc.).
266 Our analysis began with a general assessment of the impact of *Bromus* on perennial
267 grass performance using a series of one-sample t-tests. We conducted one t-test for
268 each species to compare actual growth in competition with *Bromus* to growth in a
269 hypothetical null model ($RYP = 1$). Competitive treatments were pooled across
270 *Bromus* density, *Bromus* emergence time, and nitrogen addition. We then determined
271 the effect of nitrogen availability on perennial species growth in monoculture with a
272 two-factor ANOVA, using species identity and nitrogen availability as independent
273 fixed factors. We evaluated the independent and interactive effects of *Bromus*
274 density, emergence timing, nitrogen availability, and perennial species identity with a
275 separate four-factor analysis of variance (ANOVA). We used Tukey HSD post-hoc
276 tests ($\alpha = 0.05$) to make any appropriate pair-wise comparisons in the four and two-
277 factor ANOVA tests.

278 The RYP data used in the t-tests were log transformed to improve normality
279 before analysis. Prior to application of the ANOVA tests we applied Cochran's test
280 for unequal variances to the raw data to assess its heteroscedacity. The subset of
281 biomass data used in the two-way ANOVA passed Cochran's test, so was left
282 untransformed. The RYP data used in the four-factor ANOVA failed Cochran's test.
283 We again performed a log transformation to both normalize the data and reduce
284 heteroscedacity. The transformed RYP data did not pass the test, but was closer to
285 the given critical value. Because a balanced design ANOVA, such as that employed
286 in this study, is robust to minor departures from homogeneity of variances
287 (Underwood 1997; McGuinness 2002), we proceeded with the four-factor ANOVA

288 on the transformed data. We present back-transformed data and errors in figures
289 when data were transformed for analysis.

290

291 **Results**

292 **Perennial response to *Bromus* presence**

293 Growth of all three perennial species was suppressed in the presence of *Bromus*.
294 When compared to the hypothetical control RYP value of 1, the aboveground
295 production of *Holcus* ($t = -9.983$, $df = 58$, $p < 0.0001$), *Nassella* ($t = -17.381$, $df = 63$,
296 $p < 0.0001$), and *Festuca* ($t = -23.150$, $df = 63$, $p < 0.0001$) was significantly reduced
297 when grown with *Bromus*. However, the degree to which *Bromus* affected perennial
298 growth differed among species. Competitive treatments reduced *Holcus* growth by
299 nearly 75%. The two native perennials experienced even greater suppression:
300 *Nassella* growth was reduced by 85% while *Festuca* growth was reduced by 95%
301 (Figure 1).

302

303 **Perennial response to nitrogen addition in monoculture**

304 Nitrogen availability significantly interacted with perennial grass species identity in
305 the monoculture treatments (Table 1a). *Holcus* and *Festuca*, but not *Nassella*,
306 responded to nitrogen addition with increased aboveground growth (Figure 2).
307 *Holcus* grew significantly larger than the other two perennial species: in both the
308 ambient and added nitrogen treatments *Holcus* growth surpassed *Festuca* and
309 *Nassella*, while the aboveground production of the two native grasses was statistically
310 indistinguishable (Figure 2).

311

312 **Perennial response to varying *Bromus* density, nitrogen addition, and**
313 **order of emergence**

314 There were two significant three-way interactions in the four-factor ANOVA: 1)
315 Perennial sensitivity to *Bromus* density varied with nitrogen addition and order of
316 emergence, and 2) Perennial species identity interacted with *Bromus* density and
317 nitrogen addition (Table 1b). These interactions are discussed in detail below.

318

319 *Bromus density x nitrogen addition x order of emergence*

320 Delayed *Bromus* emergence significantly increased productivity of the perennial
321 grasses (Table 1b). Positive production responses by the perennials in delayed
322 *Bromus* emergence treatments occurred at both *Bromus* densities although the
323 ‘release’ was stronger at low *Bromus* density (Figure 3). Nitrogen addition had no
324 effect on this pattern. High *Bromus* density generally resulted in lower perennial
325 grass growth, although the effect was negated in the simultaneous *Bromus* emergence
326 pots with added nitrogen (Figure 3).

327

328 *Perennial species identity x Bromus density x nitrogen addition*

329 The three perennials differed greatly in their responses to reduced *Bromus* density and
330 increased nitrogen availability (Table 1b). In the high nitrogen treatment, *Holcus*
331 RYP was significantly greater than that of *Nassella* or *Festuca* at both high and low
332 *Bromus* density (Figure 4). *Nassella* and *Festuca*, the two native species, responded
333 similarly to each other in the high nitrogen treatment. By contrast, in the low
334 nitrogen treatment *Nassella* outperformed *Festuca* and, at the high *Bromus* density,
335 outperformed *Holcus*. In the low *Bromus* density treatment, *Holcus* and *Nassella*
336 RYP were similar while *Festuca* RYP was significantly lower (Figure 4).

337 Overall, *Holcus* experienced the least growth in the high *Bromus* density, low
338 nitrogen level treatment (Figure 4). Reduced *Bromus* density and increased soil
339 nitrogen availability tended to increase *Holcus* performance (Figure 4). Like *Holcus*,
340 *Festuca* exhibited the least growth in the high *Bromus* density treatment at the lower
341 nitrogen level. Although *Festuca* growth increased in the low *Bromus* density
342 treatment, overall, *Festuca* experienced the most consistent suppression by *Bromus* of
343 the three perennial grasses (Figure 4). In contrast to *Holcus* and *Festuca*, *Nassella*
344 experienced its lowest level of growth in high *Bromus* density with high soil nitrogen.
345 *Nassella* RYP was significantly increased with reductions in either nitrogen
346 availability or *Bromus* density.

347

348 **Discussion**

349 This study gauged the importance of density and timing of emergence of an abundant
350 annual grass on potentially coexisting perennial grasses under different levels of soil
351 fertility. The annual grass competitor *Bromus* suppressed growth of all three
352 perennial species relative to their growth in monoculture. As predicted, the level of
353 suppression tended to increase with *Bromus* density and decrease when perennial

354 grasses emerged before *Bromus*. Nitrogen addition increased the suppression of one
355 native perennial by *Bromus*, while the other native perennial showed no response.
356 Suppression of the exotic perennial by *Bromus* was decreased with nitrogen addition.
357

358 **Order of emergence and density impacts on native perennial grass**
359 **seedling growth**

360 Both the native and exotic perennial grasses responded strongly to delays in *Bromus*
361 emergence, increasing relative yield per plant (RYP) up to eight-fold (Figure 3). The
362 reduced *Bromus* density treatment similarly increased perennial grass RYP. The
363 strength of these responses demonstrates the potential importance of timing of
364 emergence for perennial grass seedlings and supports findings of previous studies in
365 California grasslands and other semi-arid grassland systems that highlight the
366 sensitivity of the seedling stage in perennial grasses (Bartolome and Gemmill 1981;
367 Dyer et al. 1996; Dyer and Rice 1997; Clausnitzer et al. 1999; Hamilton et al. 1999;
368 Brown and Rice 2000; Humphrey and Schupp 2004; Lenz and Facelli 2005).
369 California native perennial grasses must survive the summer drought, and accordingly
370 invest less in their aboveground growth or reproductive efforts in the first year than
371 do exotic annual grasses (Jackson and Roy 1986; Holmes and Rice 1996). Annual
372 grasses, on the other hand, must complete their life cycle before California's annual
373 summer drought and so are among the earliest plants to germinate following the onset
374 of the rainy season. The high seedling densities and rapid aboveground growth
375 exhibited by exotic annual grasses creates an intense competitive environment for
376 later emerging seedlings (Jackson and Roy 1986; Corbin et al. 2007).

377 Priority effects have been reported in numerous systems across a broad range
378 of taxonomic groups (e.g. Harper 1961; Lawler and Morin 1993; Shorrocks and
379 Bingley 1994, D'Antonio et al. 2001; Kennedy and Bruns 2005). In California

380 grasslands, established native perennial stands are generally resistant to invasion by
381 exotic annual grasses (Seabloom et al. 2003; Corbin and D'Antonio 2004b; Lulow
382 2006), representing a priority effect manifested through arrival in a previous growing
383 season. However, priority effects for exotic annual grasses competing with perennial
384 seedlings occur over much shorter time scales. Previous work has shown that
385 differences in emergence timing of even a few days can be enough to reverse
386 competitive hierarchies between similar grass types (Harper 1961; Ross and Harper
387 1972; Rice and Dyer 2001). Some grasses, including *Nassella*, may even accelerate
388 emergence in response to annual grass neighbors, presumably to minimize the
389 impacts of later emergence (Dyer et al. 2000). Here we demonstrate the strong
390 priority effects that annual grasses can have on the seedlings of potentially coexisting
391 perennial grasses; reversing the order of emergence of the grass types had a large
392 effect on perennial grass seedling productivity, even when greatly outnumbered by an
393 exotic annual grass.

394 Early emergence and high densities of exotic annual seedlings are obstacles
395 that must be overcome for the restoration and maintenance of native-dominated
396 grasslands (Stromberg et al. 2007). Successful restoration of native perennial
397 grasslands often employs at least one of three strategies which improve perennial
398 seedling performance: increasing native seed input (e.g. Seabloom et al. 2003),
399 decreasing annual grass seed input/germination (e.g. Moyes et al. 2005), or planting
400 plugs of native perennial grasses rather than starting them from seed (e.g. Dyer et al.
401 1996; Huddleston and Young 2004). The first two strategies reduce the relative
402 abundance of exotic annual grasses, while the last, in effect, reverses the order of
403 emergence of exotic annual and native perennial grasses.

404 Once established, some stands of native perennials are able to exclude annual
405 grass invasion (Corbin and D'Antonio 2004b), and some studies suggest native

406 perennial grasses are stronger per-capita competitors than exotic annual grasses (e.g.
407 Seabloom et al. 2003; DiVittorio et al. 2007). However, the high rate of soil turnover
408 in California grasslands due to gopher and feral pig disturbance will create numerous
409 opportunities for exotic annual grasses to compete with native perennial seedlings
410 within restoration projects over the long-term (Hobbs and Mooney 1985, Kotanen
411 1995, Stromberg and Griffin 1996). Given that exotic annual propagule supply
412 grossly exceeds that of native perennials, asymmetry in competition through
413 emergence timing and density will likely limit the long-term ability of native
414 perennial grasses to reestablish dominance in restored areas unless disturbance is
415 minimized.

416

417 **Nitrogen addition impacts on native perennial grass seedling growth**

418 Differential responses to nitrogen addition between the two native perennial grass
419 species point toward differences in their ability to access this resource amidst
420 abundant exotic annual grass cover. *Nassella* in the monoculture treatment did not
421 increase aboveground growth following nitrogen addition, which suggests it was not
422 nitrogen limited in this study. Alternatively, the response could have been reflected
423 by reduced investment in belowground growth (Chapin 1980), which we did not
424 measure in this study. However, *Nassella* root:shoot did not decrease with nitrogen
425 fertilization in another study (Thomsen et al. 2006a). When nitrogen was added to
426 *Nassella* grown with a high density of *Bromus*, *Nassella* experienced a relative
427 decrease in aboveground growth. *Festuca*, on the other hand, did exhibit a positive
428 growth response to nitrogen addition in monoculture, demonstrating that it was
429 nitrogen limited. However, *Festuca* showed no response to nitrogen addition when
430 grown with *Bromus*, suggesting that *Festuca* was unable to benefit from added
431 nitrogen with neighboring annuals present. The responses of both *Nassella* and

432 *Festuca* are consistent with an indirect negative relationship between soil nitrogen
433 and native perennial grass performance due to increased productivity of exotic annual
434 grasses.

435 Our findings complement a number of studies in California and other semi-
436 arid grasslands that found that exotic annual grasses benefit disproportionately from
437 soil nitrogen supplementation relative to native perennial grasses (e.g. Huenneke et al.
438 1990; Maron and Connors 1996; Claassen and Marler 1998; Prober et al. 2002; Lowe
439 et al. 2003; Abraham et al. unpublished data; but see Kolb and Alpert 2003). This
440 suggests that native perennial grass seedlings are less likely to establish when faced
441 with both exotic annual grass competition and persistent or increasing soil nitrogen
442 enrichment. While this does not bode well for grassland restoration efforts, Seabloom
443 et al. (2003) found that, with seed supplementation, perennial grass seedlings were
444 capable of establishing in stands of exotic annual grasses across a gradient of nitrate
445 availability. However, their exotic annual grass stands were not dominated by
446 *Bromus diandrus*; it is possible that the identity of the annual grass competitor plays a
447 role in determining the outcome of perennial grass seedlings. D'Antonio and Corbin
448 (2004a) showed a first year reduction in annual grass suppression of native perennial
449 seedlings after soil amendment with sawdust (to reduce available soil nitrogen), but
450 found that there was no long-term benefit to the native grasses. Active management
451 of soil nitrogen levels may prove to be less important for maintenance of native
452 perennial dominated grasslands than reducing the density of exotic annual grass
453 competitors (DiVittorio et al. 2007).

454

455 **Comparison of exotic and native perennial grass seedling response**

456 Productivity, tolerance of annual grass competition, and response to resource pulses
457 differed significantly between native and exotic perennial grasses in this study. While

458 each perennial species responded to the inclusion of *Bromus* with marked reductions
459 in growth, *Holcus* tended to be less affected than either native perennial. Relative to
460 *Festuca*, *Holcus* suffered a smaller overall reduction in growth in every treatment
461 combination. In low nitrogen conditions, *Nassella* RYP was equal to or greater than
462 *Holcus* RYP. However, *Nassella* RYP was lower than that of *Holcus* when nitrogen
463 levels. Additionally, *Holcus* productivity was much greater than that of either native
464 perennial in monoculture (Figure 2).

465 A field study of *Holcus* establishment in exotic annual grasslands found that
466 *Holcus* seedling growth was not affected by competition with annual grasses
467 (Thomsen et al. 2006b). Thomsen et al. (2006a) also demonstrated that *Holcus* has
468 much higher initial relative growth rates than native perennial grasses, under both
469 high and low nitrogen conditions. Individual size in grasses is often positively
470 correlated with survival likelihood and competitive ability (Davies et al. 1999; Ewing
471 2002; Page and Bork 2005). As such, even if exotic annual grasses suppressed
472 *Holcus*, *Festuca*, and *Nassella* equally, *Holcus* would likely be better able to compete
473 with other grassland species due to its faster growth rate and larger size. Given the
474 results of this study and Thomsen et al. (2006b), it is likely that *Holcus* seedlings
475 better establish in exotic annual grass dominated stands than do native perennials.

476 Unlike the two native perennials, *Holcus* growth increased with additions of
477 nitrogen both in monoculture and in combination with *Bromus*, suggesting that
478 *Holcus* is a relatively strong competitor for soil resources with *Bromus*, at least when
479 water is not limiting as in this study. This response was mirrored in a field study;
480 elevated light and nutrient availability due to gopher disturbance increased *Holcus*
481 colonization relative to an exotic annual, *Vulpia bromoides* (Peart 1989c). *Holcus*
482 also showed increased productivity with higher nitrogen availability while in
483 competition with native perennial grasses (Schippers et al. 1999; Ewing 2002;

484 Thomsen et al. 2006a), so appears to be not only highly responsive to nitrogen
485 enrichment, but able to access that nitrogen alongside a range of potential
486 competitors.

487

488 **Implications for management**

489 California's annual-dominated grasslands have excluded native perennial grasses for
490 decades, but in the coastal zone are often colonized by a number of exotic perennial
491 bunchgrass species; this suggests that there are critical differences between traits of
492 these native and exotic perennial grasses. In this study the native and exotic perennial
493 grasses we investigated responded differently to both soil fertilization and
494 competition with exotic annual grasses. Currently, common strategies for native
495 grass management are based on mitigating the emergence of exotic annual grasses,
496 and the associated negative effects of nitrogen enrichment that accompany their high
497 density and rapid growth. However, management tools to specifically limit the
498 encroachment of exotic perennial grass are largely undeveloped, and the efficacy of
499 current management techniques on limiting their spread is not well known (Stromberg
500 et al. 2007). Management practices that reduce annual grass seedling density could
501 inadvertently increase the abundance of *Holcus*, particularly in areas with high soil
502 nitrogen availability. As European perennial grasses become increasingly abundant
503 and widespread in California coastal grasslands, land management based on
504 generalizable life history differences among native perennial and exotic annual
505 grasses will lose efficacy. Successful management for native grassland species will
506 require continued research into the traits of a wider range of native and exotic
507 bunchgrasses and their species-specific responses to current restoration practices and
508 future environmental conditions.

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809 Table 1. Summary of two-factor and four-factor ANOVA tests. a) Two-factor
 810 ANOVA. Effect of perennial species identity (PS) and nitrogen availability (N) on
 811 aboveground production. b) Four-factor ANOVA. Effects of perennial species
 812 identity (PS), *Bromus* emergence time (BET), *Bromus* density (BD), and nitrogen
 813 availability (N) on relative shoot yield per plant. Significant results are in bold.
 814

| a) Two-Factor ANOVA | | | | |
|------------------------------|-----|-------------|---------|------------------|
| Treatment | df | Mean-Square | F | P |
| Perennial Species | 2 | 47.808 | 161.19 | <0.001 |
| Nitrogen | 1 | 6.695 | 22.573 | <0.001 |
| PS x N | 2 | 1.841 | 6.209 | 0.004 |
| Error | 40 | 0.297 | | |
| b) Four-Factor ANOVA | | | | |
| Treatment | df | Mean-Square | F | P |
| Perennial Species | 2 | 45.797 | 32.823 | <0.001 |
| <i>Bromus</i> Emergence Time | 1 | 296.475 | 212.490 | <0.001 |
| <i>Bromus</i> Density | 1 | 26.100 | 18.707 | <0.001 |
| Nitrogen | 1 | 7.133 | 5.113 | 0.025 |
| PS x BET | 2 | 4.573 | 3.278 | 0.040 |
| PS x BD | 2 | 0.160 | 0.115 | 0.892 |
| PS x N | 2 | 15.665 | 11.228 | <0.001 |
| BET x N | 1 | 0.211 | 0.151 | 0.698 |
| BET x BD | 1 | 0.841 | 0.603 | 0.439 |
| BD x N | 1 | 5.412 | 3.879 | 0.051 |
| PS x BET x BD | 2 | 0.467 | 0.335 | 0.716 |
| PS x BET x N | 2 | 3.722 | 2.668 | 0.072 |
| PS x BD x N | 2 | 5.012 | 3.592 | 0.030 |
| BET x BD x N | 1 | 7.240 | 5.189 | 0.024 |
| PS x BET x BD x N | 2 | 1.463 | 1.049 | 0.353 |
| Error | 162 | 1.395 | | |

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821 Figure 1. Relative shoot yield of perennials (RYP) in response to competition with
822 *Bromus*, averaged across all *Bromus* density, nitrogen, and *Bromus* emergence time
823 treatments (mean \pm 1 SE). An RYP below 1 suggests a reduction in growth with
824 *Bromus* competitors relative to growth in monoculture.

825

826 Figure 2. Perennial aboveground growth in monoculture with and without nitrogen
827 addition (mean \pm 1 SE). Vertical lines indicate non-significant differences within a
828 given nitrogen treatment. Asterisks indicate differences within a single species across
829 nitrogen treatments; 'n.s.' indicates non-significance.

830

831 Figure 3. Relative shoot yield of perennials (RYP) in high and low *Bromus* density
832 treatments at simultaneous and late *Bromus* emergence times, separated by nitrogen
833 addition treatment (mean \pm 1 SE). Horizontal lines indicate non-significant
834 differences within a given nitrogen and emergence time treatment combination.
835 Shared letters indicate non-significant differences within a given density of *Bromus*
836 across nitrogen addition and emergence time treatment combinations.

837

838 Figure 4. Relative shoot yield of perennials (RYP) with and without nitrogen
839 addition, separated by *Bromus* density treatment (mean \pm 1 SE). Horizontal lines
840 indicate non-significant differences within a given density and nitrogen treatment
841 combination. Shared letters indicate non-significant differences within a single
842 species across all density and nitrogen treatment combinations.

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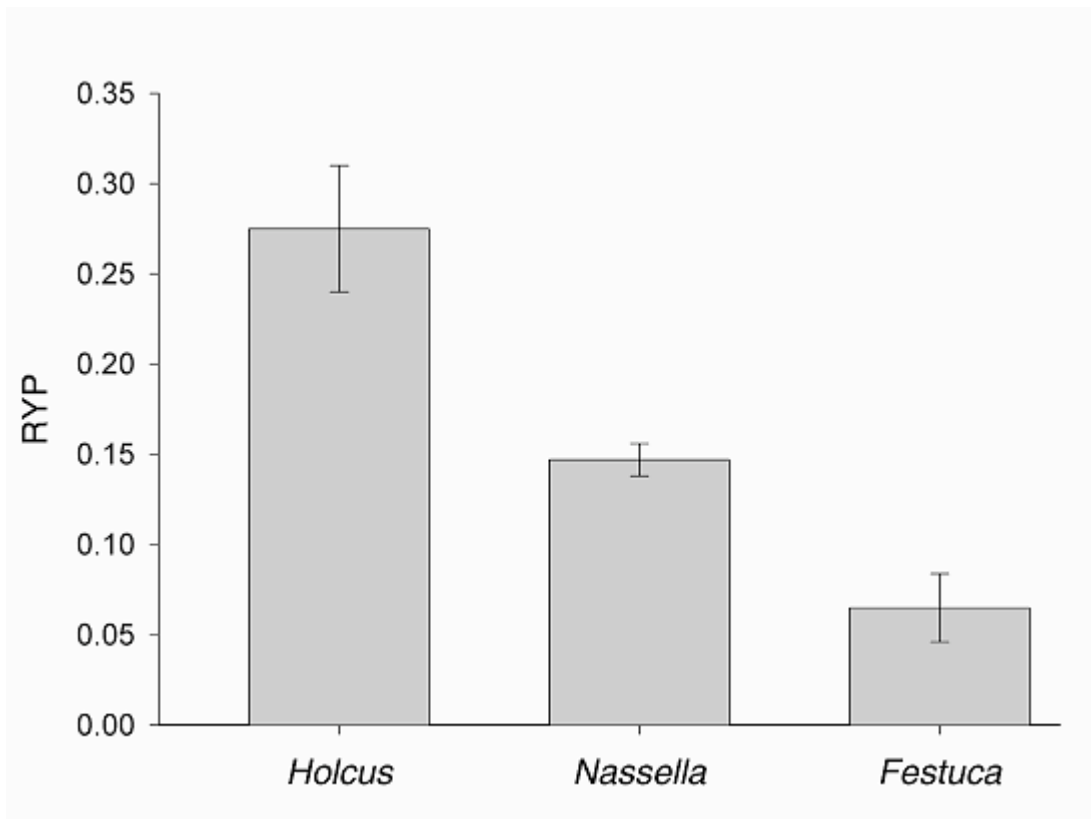
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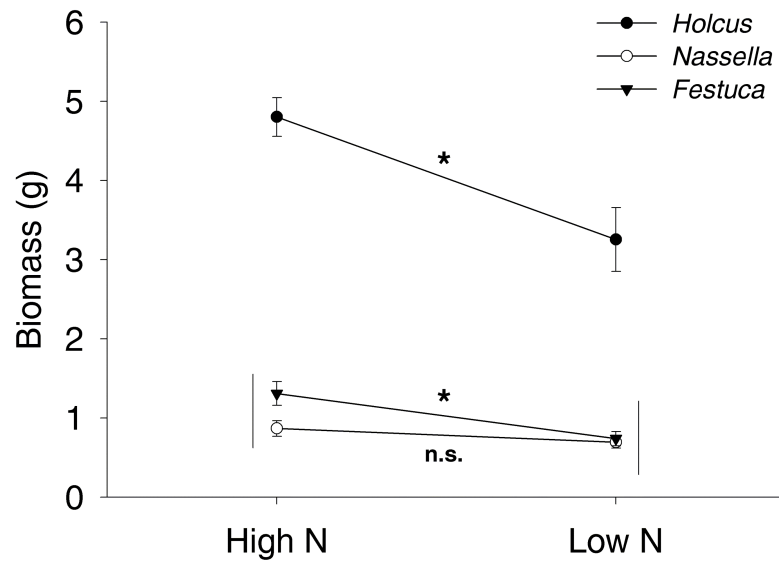
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Figure 1

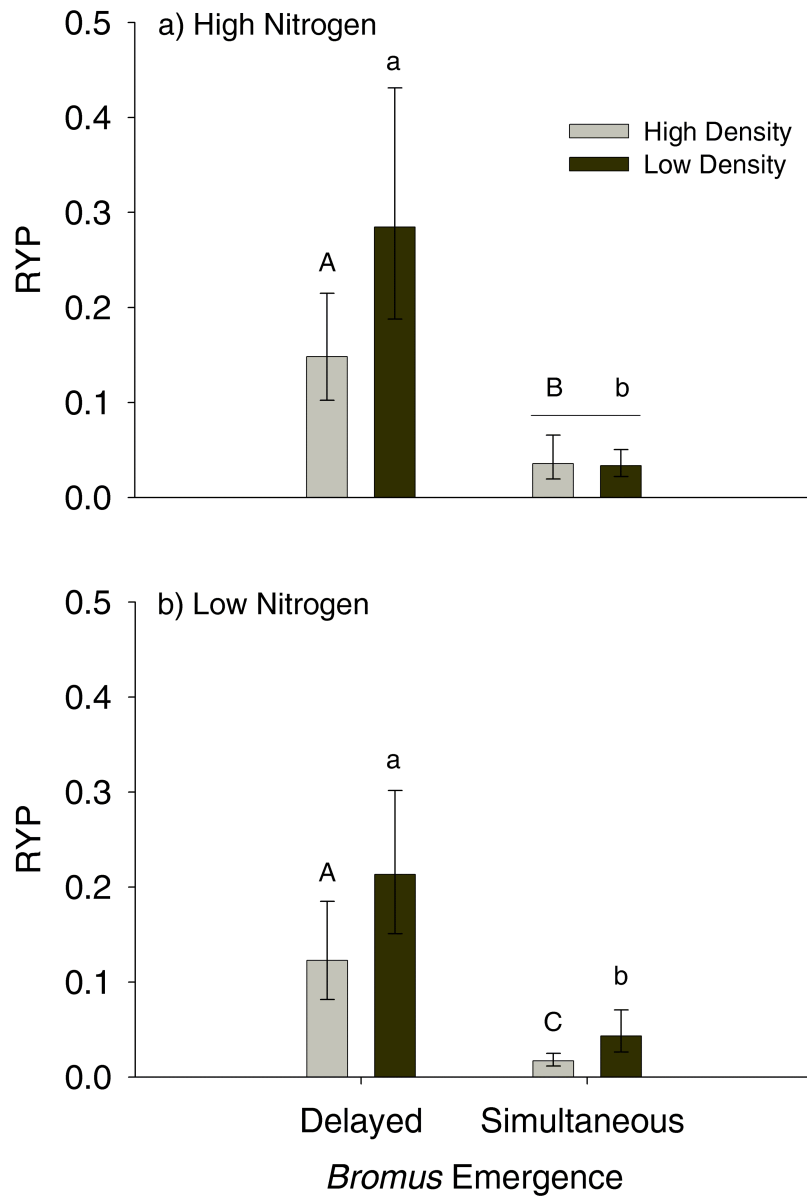


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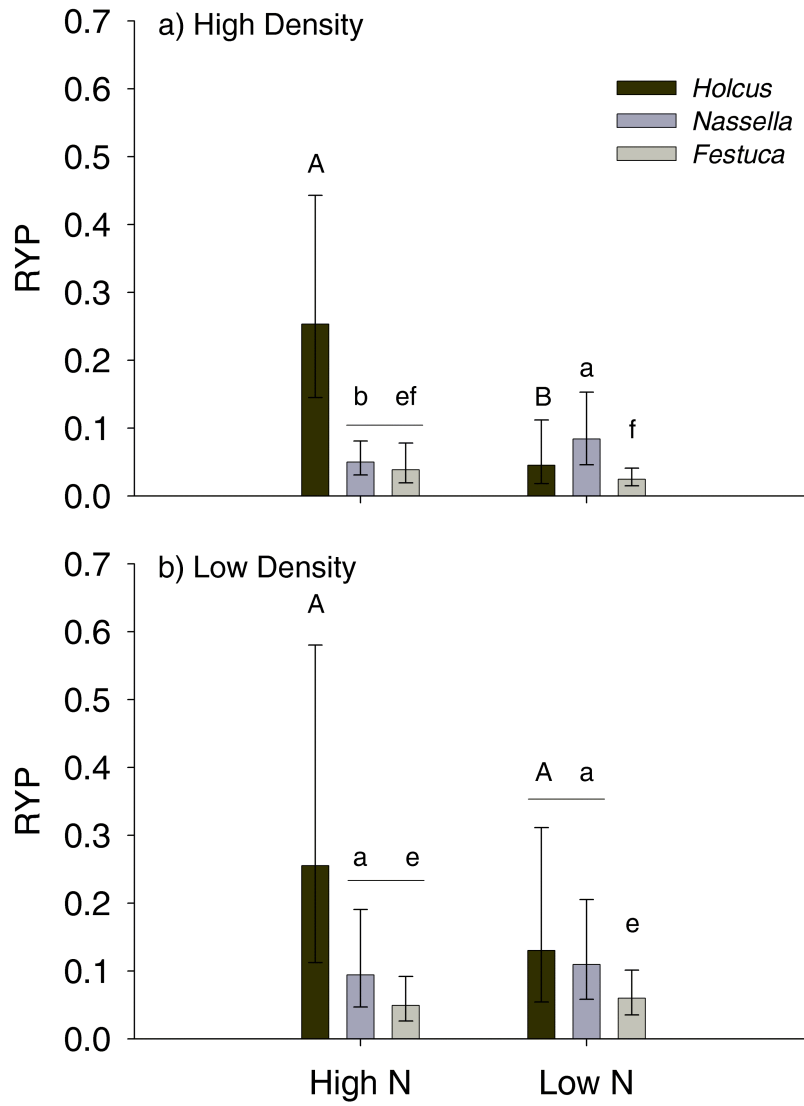
899 Figure 2



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