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Root Inputs Influence Soil Water Holding Capacity and Differentially Influence the Growth of Native versus Exotic Annual Species in an Arid Ecosystem

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15

18 **Abstract**

19

20   Invasion by exotic annual species is increasingly impacting Southern California

21 aridlands, altering ecosystem processes and plant community composition. With climate

22 change the Southwestern US is expected to experience increasingly variable rainfall.

23 Larger rainfall events could facilitate invasion by exotic species that can capitalize on

24 high resource conditions. Exotic annual species also have dense shallow root systems

25 that could create positive feedbacks to further invasion by increasing soil organic matter

26 and water holding capacity. Alternatively, fine root inputs could create negative

27 feedbacks to exotic plant growth if they stimulate microbial nutrient immobilization. The

28 dual influences of rainfall regime and fine root inputs on species performance were

29 evaluated in an experiment where native and exotic species were grown individually and

30 in combination under varying watering regimes (large infrequent or small frequent

31 pulses, holding total rainfall constant) and root additions (with or without sterilized exotic

32 roots). Mean soil moisture increased with larger infrequent watering events, and also with

33 root addition. Plant growth (both native and exotic) increased with larger watering events,

34 but declined with root addition. Exotic species growth declined more than native species

35 growth with root additions. Mechanistically, root addition lowered inorganic nitrogen (N)

36 availability, and microbial N immobilization increased with soil moisture content.

37 Together these results show that increased fine root production promotes negative

38 feedbacks to growth of exotic species via microbial N immobilization, especially under

39 conditions of high soil moisture. Further, our results suggest that organic carbon additions

40 are a potentially effective strategy for suppressing growth of problematic desert invaders.

41

42 **Introduction**

43

44   Exotic annual species are problematic invaders across western North America,

45 especially in arid and semi-arid regions (Mack 1981, Lovett & Bainbridge 1999, Craig et

46 al. 2010), where they can negatively impact native species (Barrows et al 2009) and alter

47 ecosystem functioning by accelerating the fire regime (Brooks et al. 2004, Schiermeier

48 2005). Environmental changes such as altered climate and nitrogen (N) deposition may

49   be facilitating these invasion, favoring exotic grasses over native desert species (Rao &

50   Allen 2010). Invasions may become increasingly common in these areas because the

51   Southwestern U.S. is expected to be a climate change "hot spot" in the coming decades,

52   associated with increasingly variable rainfall patterns (Diffenbaugh et al. 2008). The

53   abundance of exotic annual species often increases in high rainfall years (Hobbs et al.

54   2007, Bethany & Mustard 2005), but we know much less about how native and exotic

55   species respond to variation in the magnitude of rainfall events within years, although it

56   has been predicted that more variable rainfall regimes will promote invasion (Knapp et al.

57   2008).

58   Positive plant-soil feedbacks may plant an important role in facilitating the spread

59   of problematic invaders (Levine et al. 2006). Exotic species can alter soil microbial

60   communities (Klironomos 2002; Callaway et al. 2004), through inputs of allelopathic

61   chemicals (Bais et al. 2003; but see Lind & Parker 2010), alteration of light availability

62   via the litter layer (Lenz et al. 2003) or by altered nutrient cycling (Eherenfeld 2003;

63   Evans et al. 2001). One potential feedback mechanism that has been surprisingly untested

64   is the role of root proliferation by exotic annual species, and subsequent additions of

65   organic carbon (C) into soils. Exotic annual grasses often have high below-ground

66   production of dense, fine roots (Holmes & Rice 1996); potentially creating a positive

67   feedback, promoting invasion via by increasing soil water holding capacity.

68   Alternatively, C additions in mesic systems often increase microbial activity and hence

69   immobilization of limiting nutrients, suppressing the growth of exotic species and thus

70   favoring native species (Blumenthal et al. 2003; Perry et al. 2010). The proliferation of

71   fine root biomass associated with invasion by exotic annual species in arid and semi-arid

72   environments could thus lead to a mix of positive (via enhanced soil water holding

73   capacity) and negative feedbacks (via microbial nutrient immobilization) to growth of

74   exotic species. Here we performed a greenhouse experiment to evaluate competition

75   between exotic annual species and native desert forbs under varying soil moisture

76   regimes, both with and without added fine root biomass. We tested the following

77   hypotheses: 1) We expect all species have higher growth with higher soil moisture when

78   grown individually, but exotic species will outperform native species when grown in

79   competition under high soil moisture conditions; 2) Larger, less frequent precipitation

3

80   events maintain high soil moisture and disproportionately benefit invasive species; 3)

81   High root inputs from exotic species enhances soil water holding capacity, thus creating a

82   positive feedback to enhance invasion success; 4) Alternatively, C inputs via the roots of

83   exotic species could promote microbial activity, immobilize nutrients, and suppress plant

84   growth. We evaluated these hypotheses for a suite of species commonly found in the

85   aridlands of San Diego County, with the goal of evaluating two potential restoration

86   strategies (C addition, seeding native species) to favor native species over problematic

87   invaders.

88

89   **Methods**

90

91   The experiment was conducted in greenhouses at the University of California, San

92   Diego Biological Field Station from January to April 2013. We selected four native focal

93   annual wildflower species which commonly flower in San Diego County each spring,

94   including *Amsinckia tessellata* (bristly fiddleneck), *Malacothrix glabrata (*desert

95   dandelion), *Laesthenia californica* (California goldfields), and *Layia platyglossa* (tidy

96   tips). We selected four problematic exotic species (designated by the California Invasive

97   Plant Council) also common in San Diego County, including *Bromus hordeaceus* (soft

98   brome), *Bromus madritensis spp. rubens* (red brome), *Erodium cicutarium* (redstem

99   filaree), and *Schismus barbatus* (common Mediterranean grass). Each species was grown

100   individually as well as together in the eight species mixture (competitive environment) in

101   each watering regime (see treatment description below) and soil organic matter content

102   (five grams sterilized exotic roots versus no roots added) in a factorial block design (n=8,

103   for a total of 288 pots).

104   Pots were filled with commercially available native topsoil (sandy loam, Agri

105   Service Inc., Vista California). Exotic grass root biomass was collected from greenhouse-

106   grown plants washed free of soil and sterilized by steam autoclaving. These roots were

107   cut into ~ one cm pieces and fibe grams of root biomass were mixed into the top five cm

108   of soil in each pot in the root addition treatment. No roots were added to the control pots.

109   Seeds of the focal species were purchased commercially (S & S Seeds,

110   Carpenteria, California) and germination percentages were evaluated on watered field

111 soils prior to the start of the experiment. Each pot was sown with enough seeds to achieve

112 a target of 24 individuals, (three individuals of each species for the pots where all eight

113 species were grown in competition). Seeds were planted on January 26 and an initial

114 pulse of 500 mL of water was added on February 4. Seedlings of *E. cicutarium* (collected

115 from the UC Elliot Chaparral Reserve) were transplanted on February 7, 2013 due to

116 poor germination success in the greenhouse.

117 Subsequent watering was initiated on February 9. The small, frequent watering

118 regime added a 60 mL pulse of water every five days, and the large, infrequent watering

119 regime added a 120 mL pulse of water every 10 days. Soil moisture measurements were

120 taken daily during one 10-day watering cycle soon after seeds germinated using a Field

121 Scout TDR 100 Soil Moisture Sensor measuring the volumetric water content. Pots were

122 rotated in blocks every two weeks to account for spatial variation in greenhouse light

123 availability. Watering continued for 47 days, at which time plants were harvested after

124 showing signs of senescence. All above ground biomass was harvested from each plot,

125 dried for 48 hours at 40° C, and weighed.

126 The top five cm of soil were collected from each pot that contained all eight focal

127 species, and sieved to remove roots and debris. Potassium chloride was used to extract

128 soils for inorganic N (Keeney & Nelson, 1987) and chloroform fumigation and extraction

129 was performed to measure microbial biomass N (Brookes et al., 1985) and C (Beck et al.,

130 1997). Potassium persulfate digestion (Delia et al. 1977) was used to oxidize all organic

131 and inorganic N to nitrate, subsequently absorbance protocols (Doane & Horwath 2003)

132 were used to determine the amount of nitrate in each sample.

133

134 *Statistical Analysis*

135

136 Statistical tests were performed with R version 2.15.0 (R Development Core

137 Team 2013). Soil moisture was analyzed using a linear mixed-effect model (nlme R

138 package, Pinheiro et al. 2014) with species origin (native, exotic, or mixed), watering

139 regime (frequent or infrequent), roots (added or not added), and block as factorial fixed

140 factors and individual pot ID as a random factor to account for repeated measures. The

141 growth responses of the focal species were evaluated with a linear mixed effect model

5

142 where block, competitive environment (species grown individual versus in combination),

143 species origin (native or exotic), watering regime and roots were included as factorial

144 fixed factors and species identity nested within origin was included as a random factor.

145 Growth responses to the treatments were also assessed for each species individually using

146 a linear model where competitive environment, water and roots were included as factorial

147 fixed factors and block as a random factor. Inorganic N, and microbial N and C were

148 predicted with a linear model where the influence of watering regime and root treatments

149 were factorially assessed with block position as a random factor. We performed type II

150 analysis of deviance tests to assess statistical significance (car R package, Fox and

151 Weisberg 2011). Tukey's Honest Significant Difference tests were performed as posthoc

152 tests when interactions were identified.

153   When species were grown individually, pot biomass values were divided by eight,

154 because 1/8 of the mass of seeds of each focal species were sown in the eight species

155 competition pots, as compared to the mass planted when each species was grown

156 individually. Hence, in this analysis we compare the observed growth of species when

157 grown in multi-species communities, and compare that value to the expected biomass of

158 that species when grown individually and seeded at the same rate.

159   Additional information regarding the source and characterization of soils and

160 roots used in this experiment are provided in the Supplementary Material, along with all

161 statistical tables.

162

163 **Results**

164

165   Pots supplemented with roots and watered with larger but less frequent events had

166 higher mean (Water $\chi^2{}_1$ = 13.83, p<0.001; Roots $\chi^2{}_1$ = 19.82 p<0.001) and minimum

167 (Water $\chi^2{}_1$ = 7.94, p<0.001; Roots $\chi^2{}_1$ = 19.53, p= 0.005) soil moisture (Fig. 1B; Table

168 S1). Although we performed these measurements soon after germination at a time when

169 we expected minimal impacts of plant growth on soil moisture, species composition had a

170 small but significant effect on mean soil moisture, whereby the pots planted with all 8

171 species had slightly lower soil moisture (Mixed moisture= 5.79 cm^3/cm^3, Exotic

172 moisture= 6.42 cm^3/cm^3, Native moisture= 6.27 cm^3/cm^3; Origin $\chi^2{}_1$ = 6.21, p= 0.045;

6

173   Fig. 1C).

174   Plant performance, as measured by biomass, was significantly influenced by

175   watering regime, species origin and root additions, with interactions (Fig. 2; Table S1).

176   Watering with large, infrequent events increased plant biomass (Watering regime $\chi^2_1 =$

177   25.60, p<0.001) and this effect was greater for exotic species (Origin x Water $\chi^2_1 = 4.76$,

178   p=0.029). In contrast, root addition decreased overall plant biomass (Root addition $\chi^2_1 =$

179   3.89, p = 0.049). When roots were added there was little difference between exotic and

180   native plants while exotics produced significantly higher biomass when grown without

181   root additions (Root x Origin $\chi^2_1 = 4.41$, p= 0.036). Block was a significant effect in our

182   analysis ($\chi^2_7 = 53.24$, p<0.001), because one block had consistently lower biomass due to

183   unknown factors (data not shown).

184   Most species had higher biomass (standardized by seeding rate) when grown

185   alone than when grown in combination (significant only for the native *M. glabrata*, and

186   exotics *E. cicutarium*, and *B. hordeaceus*; Fig. 3, Table S2). However, both the native

187   forb *A. tessellata* and the exotic grass *S. barbatus* showed higher biomass when grown in

188   combination with other species (Comptetitive environment: *A. tessellata* $\chi^2_1 = 5.04$, p=

189   0.25; *S. barbatus* $\chi^2_1 = 27.17$, p<0.001; Fig. 3A & E). Species also displayed variation in

190   their responses to the experimental treatments. Qualitatively, *S. barbatus* and *A. tessellata*

191   showed the most growth under all treatments compared with other species when grown in

192   competition, suggesting that their responses likely drove the exotic and native species

193   responses respectively (Fig. 3, Table S2). Growth of *S. barbatus* was promoted by

194   infrequent watering, and this effect was greater in the pots where all species were grown

195   in combination (Water x Competition $\chi^2_1 = 6.08$, p= 0.014; Fig. 3E, Table S2). *S.*

196   *barbatus* declined with root addition in the combination pots but not when grown alone

197   (Root x Competition $\chi^2_1 = 6.47$, p= 0.011). Infrequent, large watering events also

198   increased growth for *B. madritensis*, *B. hordeaceus, L. californica M. glabrata* and *E.*

199   *cicutarium*, although this effect was only significant for the latter two species when

200   grown individually (Fig. 3, Table S2). *E. cicutarium* showed higher growth when roots

201   were added in combination pots, however when grown individually the species had

202   higher growth when no roots were added (Root x Competition $\chi^2_1 = 4.20$, p= 0.040).

203   Inorganic N availability in soils at the end of the experiment was significantly

204   influenced by an interaction between root addition and watering regime (Root x Water χ^2

205    $_1$ =5.15, p=0.23; Table S3); root addition decreased soil inorganic N availability, and this

206   effect was strongest in pots with large but infrequent watering events. Microbial biomass

207   N concentrations were also higher in pots with infrequent watering treatments (Water χ^2 $_1$

208   =13.97, p<0.001; Table S3, Fig. 4). Treatments had no significant effects on microbial

209   biomass C (Water χ^2 $_1$ =0.45, p=0.505; Root χ^2 $_1$ =0.05, p=0.825; Root x Water χ^2 $_1$ =1.04,

210   p=0.308; Table 3).

211

212   **Discussion**

213

214   We found that larger, infrequent watering events maintained higher average soil

215   moisture than when the same water quantity was applied in small, frequent events,

216   potentially because larger watering events allowed water to reach deeper soil layers,

217   hence minimizing evaporative loss (Fay et al. 2008). Higher soil moisture in turn

218   increased plant biomass; these results are consistent with a prior study in a semi-arid

219   grassland that found larger infrequent rainfall events tended to increase soil moisture and

220   plant growth (Heisler-White et al. 2009). The large, infrequent watering treatment in our

221   experiment disproportionately increased the growth of exotic species, supporting our

222   hypothesis that exotic species would outperform native species under higher soil

223   moisture. While exotic annual species can have dramatically positive responses to years

224   of high rainfall (e.g. Hobbs et al. 2007), some studies have found no impact of soil

225   moisture on direct competition between native and exotic species (Maron and Marler

226   2008) suggesting that exotic species may not always benefit more than native species

227   from high soil moisture.

228   We also found that root addition increased mean soil moisture content, consistent

229   with prior studies showing that increasing soil organic matter content can increase soil

230   watering holding capacity (Blumenthal et al. 2003); however, the increase in soil

231   moisture caused by root addition did not increase plant growth. Instead, root addition

232   suppressed plant growth. Our analysis showed root addition suppressed exotic species as

233   a group more than native species (although this was likely driven by the significant

234   response of one species – *S. barbatus*). Microbial biomass N increased with infrequent

235 watering, suggesting that larger water pulses stimulated microbial activity to a greater

236 degree (e.g. Austin et al. 2004). Inorganic N was reduced under infrequent watering and

237 root addition, consistent with the idea that soil microbes immobilized inorganic N when

238 C was added in the form of fine roots. Adding C to soils in mesic systems often causes

239 soil microbes to immobilize N, favoring the growth of native species (Blumenthal et al.

240 2003; Alpert & Maron 2000). Thus, root addition in our study may have favored slower

241 growing native species over fast growing exotic species by limiting the available N in the

242 soil (Alpert and Maron 2000, Perry et al. 2010, Bobbink 1991). Our results show that this

243 effect was greatest when soil moisture was high (infrequent but larger watering events).

244 In a study similar to ours, Blumenthal (2009) found that C additions in concert with water

245 addition reduced invasive plant growth in a semi-arid grassland system. Still, the results

246 of this study are consistent with C addition studies in the Mojave desert, showing that C

247 amendments can stimulate increased microbial N immobilization even under xeric

248 conditions (Scheffer et al 2003, Steers et al. 2011).

249   As a group, we found that exotic species in our experiment tended to

250 competitively suppress the growth of native species, but there was significant variation

251 among our focal species in their responses. In particular *A. tessellata* had the highest

252 growth among the native species when grown in competition (Fig. 3A), and actually had

253 higher biomass when grown in combination than when grown alone, suggesting this

254 species was facilitated by growing in a diverse community. Other studies have also found

255 that *A. tessellata* was robust to exotic competition (Abella et al. 2011; Brooks 2009),

256 potentially due to traits such as large seed size and early-season germination (Salo et al.

257 2005). Hence, *A. tessellata* could be an effective choice for restoration efforts attempting

258 to establish native cover via seeding, especially when there may be potential competition

259 from exotic species present in the seedbank.

260   There was also variation among the exotic focal species in their responses to the

261 experimental treatments, with potential implications for management of these

262 problematic invasive species. *E. cicutarium* growth was significantly suppressed when

263 grown in the multi-species competitive environment, suggesting that seeding native

264 species can be an effective strategy for reducing the abundance of this common desert

265 invader. *E. cicutarium* growth was also reduced by low soil moisture (our small, frequent

266 watering treatment). This species is a common invader of many arid systems but has been
267 shown to decline substantially in drought years (Blackshaw et al. 2000). Our results
268 suggest that restoration efforts employing irrigation to promote germination of native
269 seeds should be cautious to prevent over-watering in areas where *E. cicutarium* could be
270 present in the seedbank, as high soil moisture favors this exotic species over the common
271 native species used in this experiment. Timed herbicide applications have also been
272 found to be effective for managing this particularly early-active species, and are more
273 effective for increasing native cover than management efforts such as weeding that
274 disturb soils (Marushia et al. 2010).

275   *Schismus barbatus* is a common exotic grass in Southern California deserts
276 (Brooks1999) and was the dominant species in pots where our eight focal species were
277 grown in competition. Further, biomass (scaled for seeding rate) was higher for this
278 species when grown with multiple species than when grown in a monoculture; hence,
279 efforts to re-seed native species are unlikely to be successful if this strong competitor is
280 present in the seedbank. However, *S. barbatus* growth was significantly lowered by root
281 addition, suggesting that organic C addition could be a feasible management strategy to
282 combat invasions of *S. barbatus.* This problematic invader has been shown to benefit
283 from N enrichment (Brooks 2003; DeFalco et al. 2001), and a study that used sucrose
284 additions similarly found that labile C additions reduced growth of *S. barbatus* under
285 field conditions (Steers et al. 2011), thus C additions are a logical management strategy
286 with the potential to lower N availability and hence the competitive dominance of this
287 species.

288   Management efforts focused on reducing soil N availability have generally used
289 sawdust or mulch as sources for C addition (Wilson & Gerry 1995; Zink & Allen 1998;
290 Alpert & Maron 2000; Paschke et al. 2000; Blumenthal et al. 2003). The results of this
291 study suggest that the biomass of exotic annual species could be left in situ as a C source,
292 provided it is harvested before the plants set seed, and there is not a danger of re-
293 sprouting from intact root stocks. However, exotic litter can be a fuel source promoting
294 fire, and so fuel reduction is a major goal for many land managers (Brookes et al. 2004),
295 hence management efforts aimed at maintaining litter with the goal of lowering soil N
296 availability would need to consider associated fire risks of this strategy. Additionally the

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timing of C amendments could be important: Early season C amendments are likely to

disproportionately suppress exotic annual species in this region (Salo 2004), because they

generally have flexible germination cues that allow them to emerge earlier and faster at

the start of the growing season (Wainwright & Cleland 2013). Consistent with this idea,

Steers et al. (2011) found that C amendment reduced exotic annual grass abundance most

in a year when they germinated first, while native species and exotic annual forbs were

impacted in a year when the timing of C amendment coincided with their emergence.

Overall, the results of this study demonstrate how inputs of organic C from the

fine roots of exotic species can initiate a complex set of positive and negative feedbacks

to invasion, and that the outcome of these interactions depends on environmental context

(rainfall regime), biotic interactions (interspecific competition), and species identity. In

particular, while we found that exotic species benefited more from high soil moisture

(resulting from larger, but less frequent watering events), exotic species growth declined

more than native species when roots were added to soil, even though root additions also

increased soil moisture. This shows that in this case, the negative effect of microbial

nutrient immobilization outweighed the positive influence of increased soil moisture for

plant growth when exotic roots were added to soil. Although our results highlight general

mechanistic feedbacks that may be applicable for understanding the outcome of invasions

in many systems, we also found significant variation among species in their responses to

our experimental treatments – both within and between groups based on native versus

exotic origin – that may aid in identifying effective management strategies for

particularly problematic desert invaders.

Implication for Practice

- Carbon additions in arid environments can reduce exotic plant growth via enhanced
  microbial nutrient immobilization; this effect varies among species and is greatest
  when soil moisture is high.
- *Schismus barbatus* growth was significantly suppressed by C addition, suggesting this
  would be a successful strategy to suppress growth of this invasive species.
- *Erodium cicutarium* was suppressed by interspecific competition, suggesting that

11

327   seed addition could be a strategy to combat this problematic invader.

328   • *Amsinckia tessellata* was a strong competitor with exotic plant species; this

329   widespread species is found in a variety of arid and semi-arid California vegetation

330   types, suggesting this species is a prime candidate for seeding in restoration.

336

337   **References**

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466
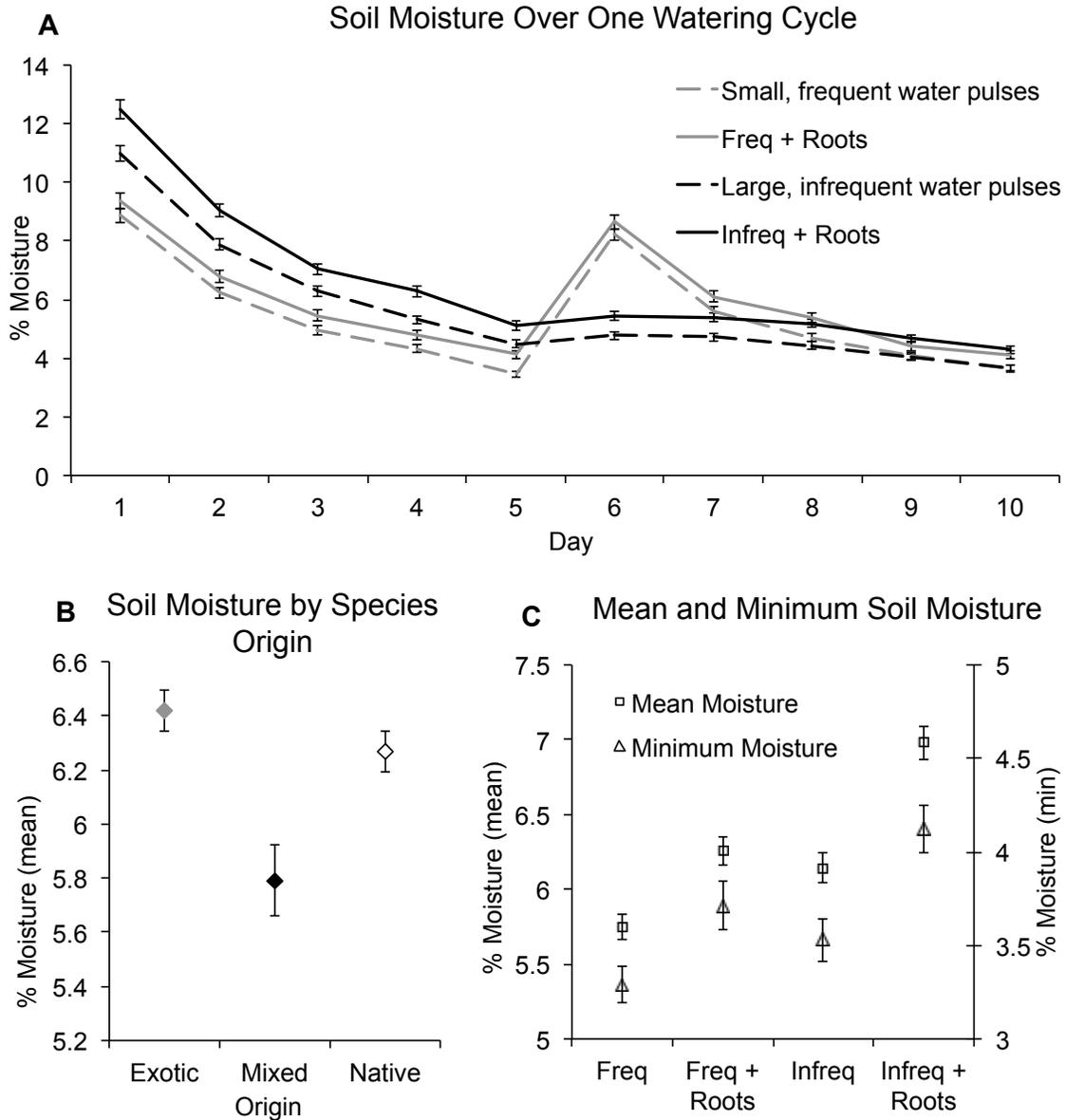
Figure 1. Mean and min soil moisture levels for one watering cycle (10 days), in each of the treatments manipulating watering regime and root additions. In the small frequent watering regime 60 mL of water was added every 5 days, while the infrequent watering regime received a single 120 mL pulse every 10 days.
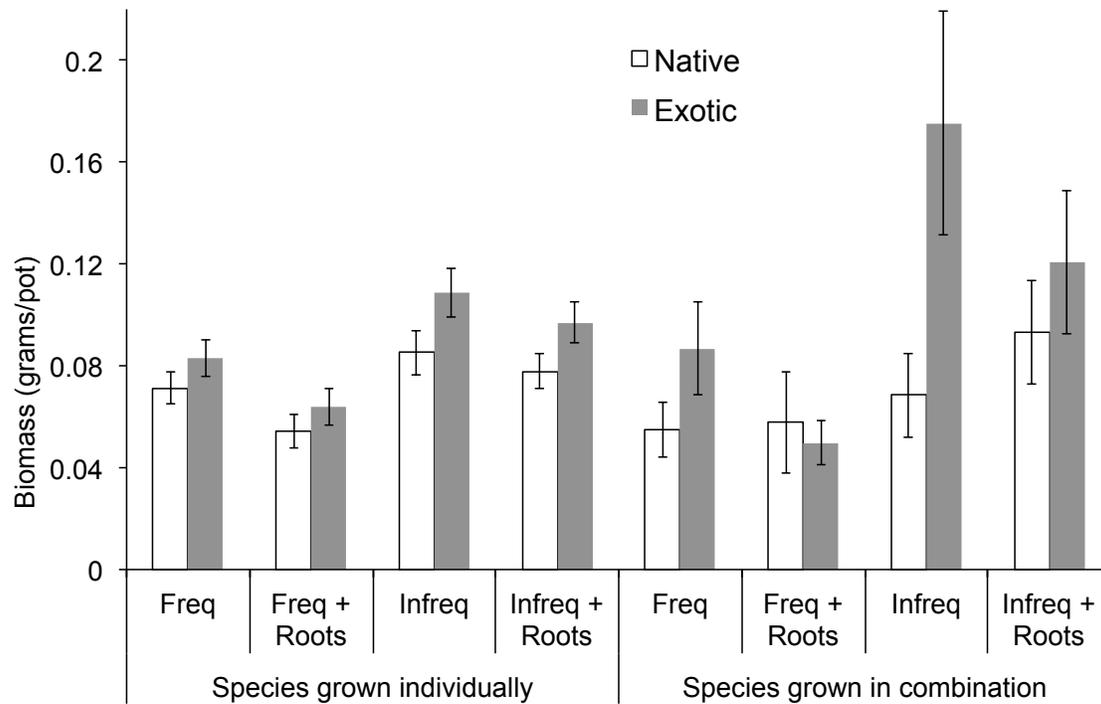
Figure 2. Above-ground biomass (mean +SE) for native and exotic species grown individually and in competition, for each treatment combination of root addition and watering frequency. Note biomass values are averaged across species to illustrate the statistical significance of the factors in the analysis.

A — *A. tessellata*

B — *L. californica*

C — *L. platyglossa*

D — *M. glabrata*

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E   *S. barbatus*

F   *B. madritensis*

G   *B. hordeaceus*

H   *E. cicutarium*

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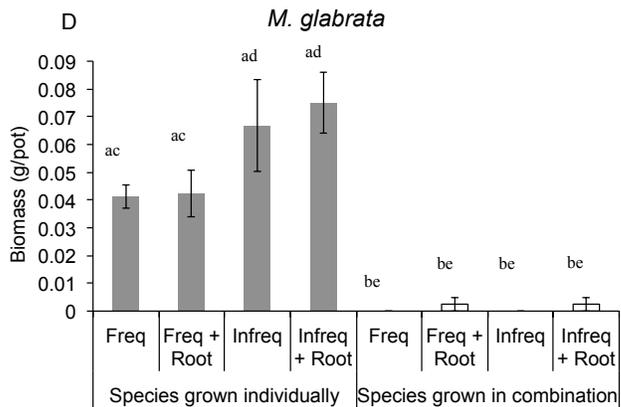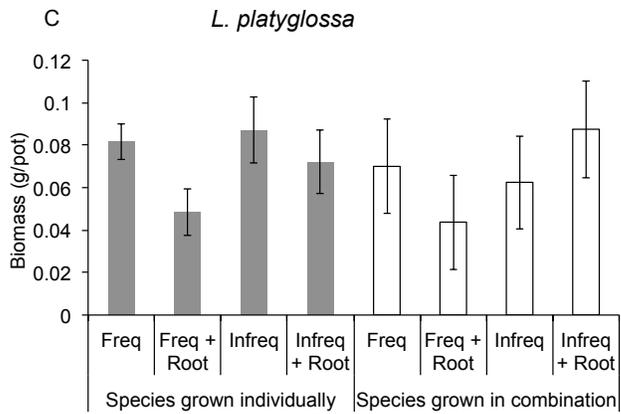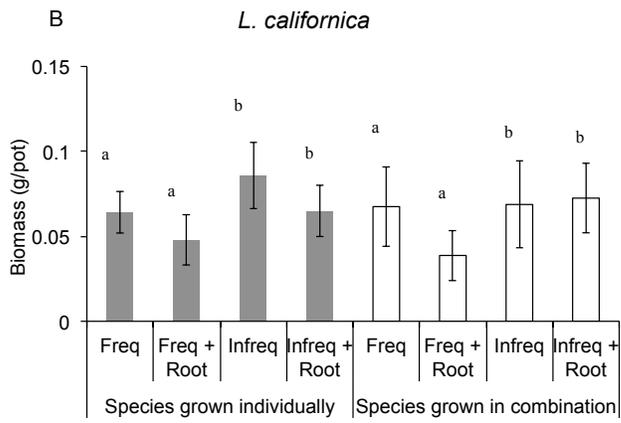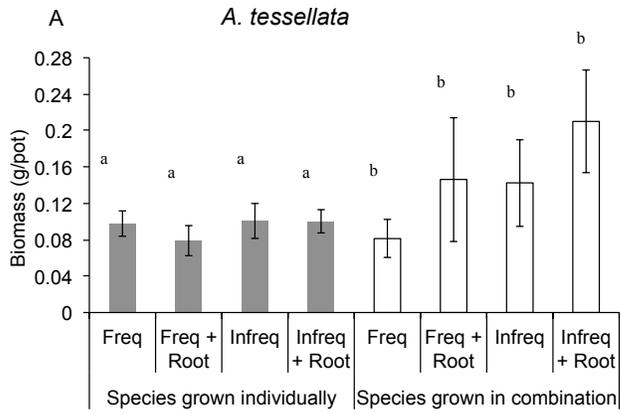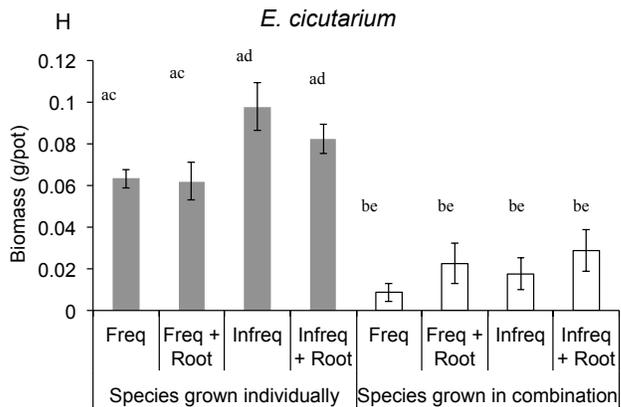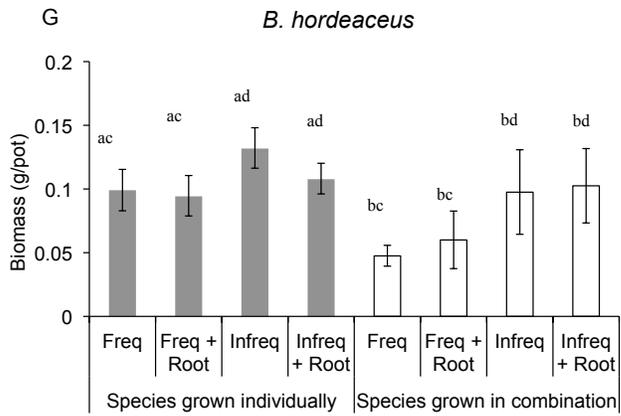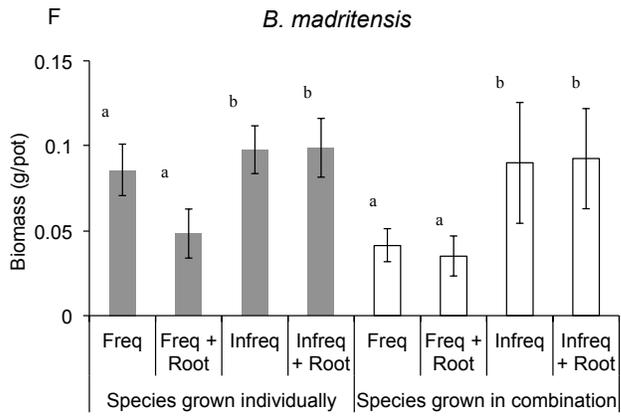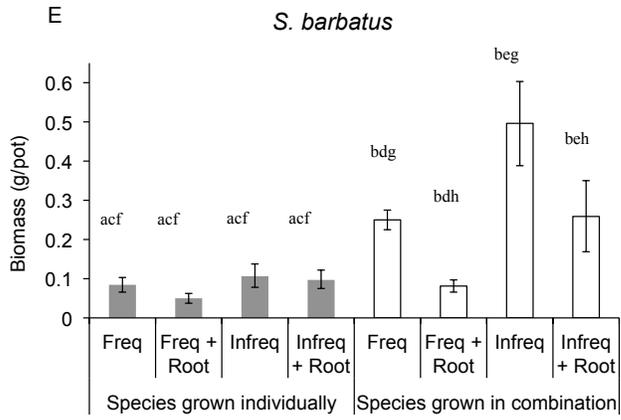
481   Figure 3. Above-ground biomass responses to varying watering regime and root addition

482   treatments for native (A- D) and exotic (E-H) species grown individually (grey) or in

483   interspecific competition with the other focal species (open).

484

A. Total Inorganic Nitrogen

B. Microbial Biomass Nitrogen
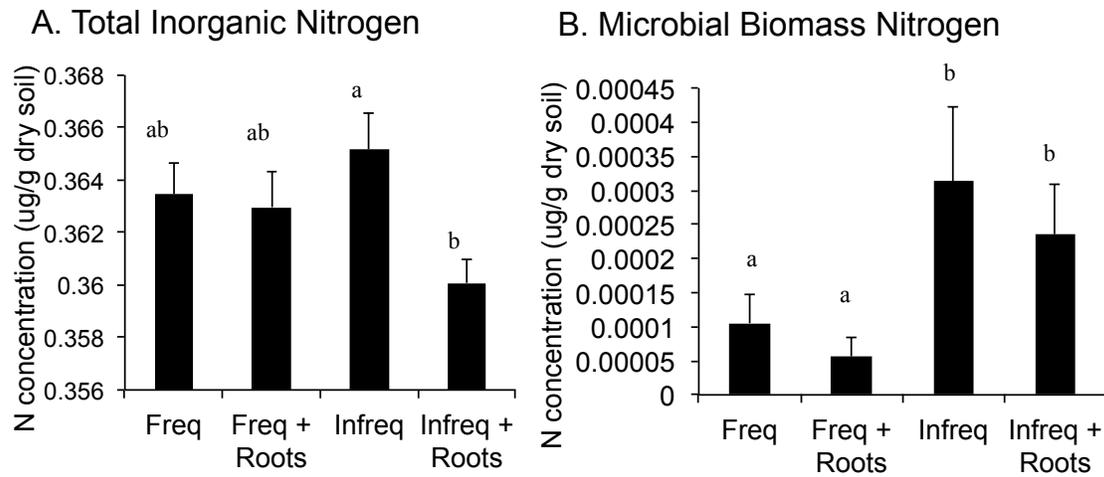
485
486 Figure 4. Concentrations of soil extractable inorganic nitrogen (A) and microbial biomass

487 nitrogen (B) for combination of watering regime and root addition treatments. Letters

488 distinguish significant differences between means based on post-hoc tests.