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# DRI-Grass: a new experimental platform for addressing grassland ecosystem responses to future precipitation scenarios in south-east Australia

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### ***Conflict of interest statement***

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

### ***Author contribution statement***

SP, SJ, UN and DT designed and led set up of the experimental facility. SP contributed to data collection and analysis, and led overall data interpretation and writing. UN led nematode/ microarthropod data collection, analysis and interpretation and assisted with writing. SJ led plant Si data analysis and interpretation and assisted with writing. DT contributed to data interpretation and writing. KB implemented root herbivore treatments, led collection of vegetation and scarab data, contributed substantially to data analysis and also writing. RO and EG-F contributed to field data collection and assisted with writing. SF led aboveground invertebrate sampling and analysis, and contributed to writing. SH ran foliar Si analyses, and contributed to data interpretation and writing.

### ***Keywords***

Climate Extremes, community ecology, drought, NPP, plant-herbivore interactions, rainfall manipulation, root herbivory

### ***Abstract***

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and contrasting levels of root herbivory

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(Authors are required to state the ethical considerations of their study in the manuscript including for cases where the study was exempt from ethical approval procedures.)

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1 **DRI-Grass: a new experimental platform for addressing**  
2 **grassland ecosystem responses to future precipitation**  
3 **scenarios in south-east Australia**

4

5

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22 **Abstract**

23

24 Climate models predict shifts in the amount, frequency and seasonality of rainfall.

25 Given close links between grassland productivity and rainfall, such changes are likely

26 to have profound effects on the functioning of grassland ecosystems and modify

27 species interactions. Here, we introduce a unique, new experimental platform - DRI-

28 Grass (Drought and Root herbivore Interactions in Grasslands) – that exposes a south-

29 eastern Australian grassland to five rainfall regimes (Ambient (AMB), increased

30 amount (IA, +50%), reduced amount (RA, -50%), reduced frequency (RF, single

31 rainfall event every 21 days, with total amount unchanged) and summer drought (SD,

32 12-14 weeks without water, December-March)), and contrasting levels of root

33 herbivory. Incorporation of a belowground herbivore (root-feeding scarabs) addition

34 treatment allows novel investigation of ecological responses to the twin stresses of

35 altered rainfall and root herbivory.

36

37 We quantified effects of permanently installed rain shelters on microclimate by

38 comparison with outside plots, identifying small shelter effects on air temperature (-

39 0.19°C day, +0.26°C night), soil water content (SWC; -8%) and photosynthetically

40 active radiation (PAR; -16%). Shelters were associated with modest increases in net

41 primary productivity (NPP), particularly during the cool season. Rainfall treatments

42 generated substantial differences in SWC, with the exception of IA; the latter is likely

43 due to a combination of higher transpiration rates associated with greater plant

44 biomass in IA and the low water-holding capacity the well-drained, sandy soil.

45

46 Growing season NPP was strongly reduced by SD, but did not respond to the other  
47 rainfall treatments. Addition of root herbivores did not affect plant biomass and there  
48 were no interactions between herbivory and rainfall treatments in the first year of  
49 study. Root herbivory did, however, induce foliar silicon-based defences in *Cynodon*  
50 *dactylon* and *Eragrostis curvula*. Rapid recovery of NPP following resumption of  
51 watering in SD plots indicates high functional resilience at the site, and may reflect  
52 adaptation of the vegetation to historically high variability in rainfall, both within- and  
53 between years. DRI-Grass provides a unique platform for understanding how  
54 ecological interactions will be affected by changing rainfall regimes and, specifically,  
55 how belowground herbivory modifies grassland resistance and resilience to climate  
56 extremes.

57  
58  
59  
60 **Key words:** Climate extremes, community ecology, drought, NPP, plant-herbivore  
61 interactions, rainfall manipulation, root herbivory

## 62 63 64 65 **Introduction**

66  
67 Grasslands cover more than 40% of the Earth's land surface (Williams *et al.*, 1968).  
68 Many support tremendous biodiversity, underpin grazing and animal production, and  
69 store more than one-third of global terrestrial carbon stocks (Trumper *et al.*, 2009).  
70 Given the close relationship between rainfall and both the productivity and diversity of

71 grasslands (Sala *et al.*, 1988; Walter *et al.*, 2012), future changes in rainfall regimes  
72 are likely to have a substantial impact on the ability of grasslands to provide these  
73 important ecosystem services.

74

75 Climate models predict changes in the overall amount and seasonality of rainfall, and  
76 increased intervals between rain events (i.e. reduced rainfall frequency) (Easterling *et al.*,  
77 2000; IPCC 2013; Fischer *et al.*, 2013). Of particular note is the expectation that  
78 prolonged and more intense droughts, in combination with warmer temperatures, will  
79 combine to expose ecosystems to more frequent extreme climates, pushing today's  
80 ecosystems into uncharted climate territory (Kayler *et al.*, 2015). The seasonality of  
81 rainfall inputs is also a crucial determinant of grassland dynamics, with seedling  
82 establishment, productivity and senescence all influenced by the amount and timing of  
83 growing season rainfall (Huxman *et al.*, 2004). Indeed, even small increases in winter  
84 rainfall have been shown to influence the functioning of grassland ecosystems in the  
85 following spring (Fry *et al.*, 2014a). Furthermore, there is a growing body of evidence  
86 that reductions in the frequency of rainfall events are at least as (and sometimes more)  
87 important as reductions in the size of events, in terms of their effects on key ecological  
88 processes (Fay *et al.*, 2003; Knapp *et al.*, 2008; Heisler-White *et al.*, 2009; Peng *et al.*,  
89 2013).

90

91 Shifts in rainfall regimes are not only expected to have a major impact on the  
92 composition and functioning of grasslands (Fry *et al.*, 2016), but are also likely to  
93 modify interactions between plants and their associated herbivores (Staley *et al.*, 2007;  
94 Johnson *et al.*, 2011; Lee *et al.*, 2014). Invasive root-feeding scarab beetles were  
95 accidentally introduced to Australia in the first part of the twentieth century (recently

96 reviewed by Frew *et al.* 2016) and, in pastures, their collective mass can exceed that of  
97 mammals grazing aboveground (Britton 1978). Because root herbivory is hidden and  
98 occurs by attrition, losses in primary productivity are less conspicuous than those due  
99 to aboveground herbivory, but can be up to 25% in grassland systems (Seastedt &  
100 Murray 2008). Even minor root herbivory can damage plants and alter their  
101 physiology by: (i) decreasing nutrient and water uptake, (ii) causing disproportionate  
102 resource losses by severing roots, (iii) diverting assimilates away from shoot growth  
103 for root re-growth, (iv) imposing leaf water deficits, and (v) causing infection  
104 (Johnson & Murray 2008; Zvereva & Kozlov 2012). The resulting effects on plant  
105 biomass and metabolism are often larger (Meyer *et al.* 2009) and differ from those  
106 caused by aboveground herbivores (Zvereva & Kozlov 2012). Impairment of root  
107 function via root herbivory has parallels with water stress imposed via periods of  
108 drought. Indeed, a recent meta-analysis has shown that root herbivory and drought  
109 reduced plant growth to a greater extent than any other combination of biotic and  
110 abiotic stresses (Zvereva & Kozlov 2012). Moreover, root herbivory can change plant  
111 community composition in grasslands via preferential feeding on certain plants  
112 (Schallhart *et al.*, 2012).

113

114 DRI-Grass (**D**rought and **R**oot Herbivore **I**nteractions in a **G**rassland Ecosystem) is a  
115 new experimental platform designed to examine ecosystem responses to the twin  
116 stresses of altered rainfall and root herbivory. Uniquely, DRI-Grass includes shifts in  
117 the size, frequency and seasonality of rainfall events, and incorporates a factorial  
118 belowground herbivore addition treatment to investigate interactions between these  
119 abiotic and biotic stresses. It joins a new generation of drought experiments (*sensu*  
120 Thompson *et al.*, 2013) that incorporate realism in terms of both future rainfall



121 scenarios (e.g. Jentsch *et al.*, 2007; Hoover *et al.*, 2014; Knapp *et al.*, 2015) and also  
122 trophic complexity (Johnson *et al.* 2011, 2015; Zhu *et al.*, 2014). Despite the clear  
123 importance of root herbivores for the functioning of grassland ecosystems (Frew *et al.*  
124 2016), their role in moderating grassland resistance and resilience under changing  
125 rainfall regimes has rarely been examined in long term field-scale experiments.

126

127 Here we introduce DRI-Grass, presenting microclimatic data that demonstrate the  
128 impacts of shelter infrastructure on the physical and biotic environment. We also  
129 present data on early vegetation responses to test the hypotheses that: 1) reduced  
130 rainfall amount and summer-long drought, will reduce aboveground productivity to a  
131 greater degree than a shift in rainfall frequency towards fewer, but larger events (with  
132 annual rainfall amount unchanged); and 2) root herbivory will alter plant quantitative  
133 (e.g. ANPP) and qualitative (e.g. chemical) responses to altered rainfall regimes. In  
134 focusing on our approach and methodology, this paper aims to provide the  
135 methodological detail that will assist other researchers interested in constructing  
136 experimental platforms that incorporate both biotic and abiotic stressors. Presentation  
137 of selected early results is intended to provide a broad indication of the ecosystem  
138 responses that can be measured using this multi-stressor, multi-trophic approach.

139

140

#### 141 **The DRI-Grass experimental platform**

142

143 The study site is located in Richmond, New South Wales, Australia (S33 36'35, E150  
144 44'18), at an elevation of 25m a.s.l. Mean annual rainfall at the site is 806 mm  
145 (Australian Government Bureau of Meteorology, Richmond - UWS Hawkesbury

146 Station; <http://www.bom.gov.au>), with summer being the wettest season and winter  
147 generally the driest. Seasonal mean maximum/minimum temperatures are 29.4/18.8 °C  
148 in summer and 17.3/3.2 °C in winter. The soil is a Blackendon Sand, with a sandy  
149 loam texture and a water holding capacity of 20-22%. There is a mineral hardpan  
150 present at approximately 90 cm depth. Table 1 summarises the soil characteristics of  
151 the site.

152

153 The experiment is situated within a former pasture grassland, comprising a total of 62  
154 plant species (Table S1), of which ~12 species are common. The most abundant  
155 species include the C<sub>4</sub> grasses *Axonopus fissifolius*, *Cynodon dactylon*, *Cymbopogon*  
156 *refractus*, *Eragrostis curvula* and *Paspalum dilatatum*, the C<sub>3</sub> grasses *Microleana*  
157 *stipoides* and *Lolium perenne*, and the C<sub>3</sub> forbs *Hypochaeris radicata* and *Plantago*  
158 *lanceolata*. The site had been under grazing management until 2001; since this time  
159 grazers were removed, the site was fenced and subsequently mown every 2-3 months,  
160 until the experiment commenced in June 2013.

161

162

### 163 **Rainout shelter design**

164

165 Shelter frames are made from 25 mm galvanized steel tubing and covered with a  
166 single sheet of clear Acrylic cast Perspex (1.88 m x 2.49 m, Mulford Plastics,  
167 Silverwater, NSW, Australia). Roofs are at a maximum height of 140 cm, sloping at a  
168 20° angle down to a low-end height of 70 cm (Figure 1). Shelters are orientated along  
169 a SW-NE axis, with the low end facing into the direction of the prevailing wind. All  
170 rainfall is intercepted and directed away from the plots. Water treatments are applied

171 following each rainfall event, using an irrigation system controlled by a Campbell  
172 logger (CR1000) and a series of 16-Channel AC/DC Relay Controller units (SDM-  
173 CD16AC units; Campbell Scientific, Thuringowa, QLD, Australia) that control  
174 solenoid valve opening/closure, and thus regulate delivery of water to individual plots.  
175 To simulate rainfall patterns that reflect actual rainfall events, the amount of water  
176 delivered is proportionate to the amount of precipitation that has fallen in the previous  
177 24 hours (i.e. AMB receives the same amount of rainfall as measured at the site in the  
178 previous 24 h; IA receives 50% more; and RA receives 50% less than the ambient  
179 amount). Target amounts of water are set using a calibrated flow meter. Water is  
180 delivered to each plot via a network of polyethylene pipes and four 90° spray heads  
181 per plot, mounted at a height of 30-45 cm (moveable, depending on vegetation height)  
182 at the corners of each shelter. An impermeable root barrier is installed within each  
183 plot, just inside the roof footprint, to a depth of 30 cm, giving an actual plot size of 1.8  
184 m x 2.0 m (i.e. 3.6 m<sup>2</sup>). This barrier prevents incursion of roots from outside the  
185 experimental plots and minimizes horizontal water flow between plots and the  
186 surrounding grassland area.

187

188

### 189 **Environmental monitoring**

190

191 Rainfall is measured using a tipping bucket rain sensor (0.2 mm graduation, ICT  
192 International, Armidale, NSW, Australia) and air temperature is measured on site  
193 every five minutes (model 107 sensor, with radiation shield, Campbell Scientific,  
194 Thuringowa, QLD, Australia). Photosynthetically active radiation (PAR) is recorded at

195 15 minute intervals (Apogee sensors, model SQ-110, ICT International, Armidale,  
196 NSW, Australia), under three shelters and in three unsheltered (outside) plots.  
197  
198 Soil moisture TDR probes (CS616, Campbell Scientific, Thuringowa, QLD, Australia)  
199 with 30 cm long prongs are installed at an angle of 30°, to integrate moisture readings  
200 for the top 15 cm of the soil profile, in half of the plots (n=3 per treatment  
201 combination). Regular (approximately every 4-6 weeks) measurements of soil  
202 moisture are also conducted manually in all plots, using a theta probe (Delta T  
203 Devices, UK), to determine whether automatically logged moisture readings from  
204 permanently sensed plots are representative of the respective treatments.  
205  
206 Given the open-sided nature of the shelters and the potential for rain ingress under  
207 windy conditions, edge effects on soil moisture were quantified under a range of  
208 conditions, including during dry periods and after small, medium and large rainfall  
209 events. Soil moisture (0-10 cm depth) was measured using a theta probe inserted in a 5  
210 x 5 grid system, covering 25 points per plot, evenly spaced at a distance of 40 cm from  
211 the plot boundary and 40 cm from the next grid point. These within-plot measurements  
212 were compared with readings taken immediately outside of the shelters (eight  
213 replicates – two along each side of the plot).

214

215

## 216 **Experimental design**

217

218 The experiment comprises five different rainfall treatments, three of which are crossed  
219 with a root herbivory treatment (detailed below). All treatment combinations are

220 replicated six times, in a fully randomized block design (n=48 (i.e. 8 x 6) for sheltered  
221 plots). There are also 12 unsheltered plots (hereinafter referred to as “Outside Plots  
222 (OP)) - six with herbivore additions and six without the addition of herbivores -  
223 making a total of 60 experimental plots.

224

225 Rainfall treatments comprise: a) sheltered control (AMB), b) reduced rainfall amount  
226 (RA: 50% reduction of ambient), c) reduced rainfall frequency (RF: ambient rainfall  
227 amount, as a single application once every 21 days), d) increased rainfall amount (IA:  
228 50% increase of ambient, and e) summer drought (SD: complete removal of all rainfall  
229 for a 12-14 week period, December-March, with ambient rainfall thereafter).

230 Unsheltered (outside control) plots (OP) receiving ambient rainfall were also included  
231 to evaluate the magnitude of shelter effects. Rainfall treatment effects were assessed  
232 by comparing the four altered scenarios (RA, RF, IA and SD) to the sheltered control  
233 plots (AMB). Rainfall treatments commenced on 21st June 2013.

234

235 Root herbivore treatment: Three of the rainfall treatments (AMB, RA, RF) and OP  
236 also include a belowground herbivore addition treatment (n=6 for each treatment  
237 combination). To impose the herbivore addition treatment, 27 g of locally collected  
238 adult scarab beetles (Coleoptera: Scarabaeidae) were added to the herbivore addition  
239 plots in December 2013, and an additional 9 g of adult beetles were added to each plot  
240 in February-March 2014. Adult beetles were added to plots by placing them within  
241 mesh enclosures in the plots, and allowing them to oviposit for a period of three days  
242 on each occasion, before mesh enclosures were removed. In order to control for the  
243 effects of the mesh enclosures on vegetation, identical structures were placed on paired  
244 (herbivore-free) plots at the same time. We verified the efficacy of herbivore

245 treatments 18 months after beetle additions (October 2015) via destructive, within-plot  
246 soil excavation and associated sampling. This involved excavating two holes (25 cm x  
247 10 cm) per plot to a depth of 20 cm; samples were separated into two depths: 0-10 cm  
248 and 10-20 cm, and sieved. Macro and mesofauna were collected, identified under a  
249 dissecting microscope and counted.

250

251

## 252 **Coordinated sampling campaigns**

253

254 We undertake regular, coordinated sampling campaigns, both above- and  
255 belowground, to determine treatment impacts on plant, microbial and invertebrate  
256 communities, and associated changes in ecosystem properties and processes. Details of  
257 these sampling campaigns are outlined below, with selected data presented in this  
258 methods paper; further data characterizing above- and belowground responses will be  
259 presented in subsequent publications.

260

## 261 ***Vegetation monitoring***

262

263 Non-destructive vegetation cover measurements are conducted approximately every 4  
264 months by placing a 1m<sup>2</sup> quadrat with 25 sub-divisions in the centre of each plot and  
265 recording species level presence/absence data in each sub-division. Since October  
266 2013, twice-yearly harvests (April and October) of all aboveground plant material  
267 have been undertaken. For this, vegetation is cut to ground level within the central 1m<sup>2</sup>  
268 of each plot and, in a randomly selected subsample (20-40% of the harvested  
269 material), live (green) material is sorted to species level and separated from dead

270 biomass. All plant material is oven-dried at 80°C for 48 hours, and weighed to provide  
271 a measure of growing season (Oct-April) and cool season (April-Oct) productivity for  
272 all plots.

273

#### 274 *Invertebrate monitoring*

275

276 Immediately prior to the harvests in October 2013, April 2014 and October 2013,  
277 aboveground invertebrates were sampled from each of the plots using a ‘G-Vac’  
278 suction sampler (SH 86C, Stihl AG & Co. KG, Germany). The device was passed over  
279 the plots in a zigzag pattern for 20 seconds, with all dislodged material and  
280 invertebrates captured in a fitted organza bag. In addition, quarterly from October  
281 2016 until April 2015, yellow sticky card traps (Bugs for Bugs, Mundubbera,  
282 Australia) were suspended from the centre of each shelter roof (or at the same height  
283 for unsheltered controls) for a period of one week to capture flying invertebrates.  
284 Invertebrates from both suction samples and sticky traps were identified to at least  
285 Order level (except for two groups taken to Subclass only – Acari and Collembola).

286

287 To quantify belowground invertebrate responses to altered rainfall regimes, two  
288 composite soil samples, each composed of two soil cores (3 cm diameter, 10 cm  
289 depth) are collected at the beginning (October) and end (April) of each growing season  
290 for extraction of soil nematodes and microarthropods. We focus on these two groups  
291 as they are the two most abundant soil invertebrate groups. Nematodes and  
292 microarthropods are extracted using standard techniques (Baermann, 1917; Tullgren,  
293 1918). Nematodes are classified to trophic level based on morphology under an  
294 inverted microscope, and counts converted to individuals per kg dry soil.

295 Microarthropods are initially sorted into springtails, oribatid, mesostigamatid and other  
296 mites (for more detail see Nielsen *et al.*, In Press). More detailed analyses will be  
297 undertaken on archived samples over the course of the experiment. Further  
298 assessments of soil invertebrate groups that require more destructive sampling  
299 campaigns will be undertaken at a later stage in the experiment to avoid substantial  
300 disturbance.

301

### 302 ***Plant, soil and microbial analyses***

303

304 Leaf material was sampled from three grass species (*Cynodon dactylon*, *Eragrostis*  
305 *curvula* and *Microlaena stipoides*) in November 2014 and analysed for silicon  
306 concentrations. Ground plant material was pressed at 11 tons into 5 mm thick  
307 cylindrical pellets with a manual hydraulic press using a 13 mm die (Specac,  
308 Orpington, UK). Si concentration (% dry mass) was determined using a commercial P-  
309 XRF analyser (Niton XL3t900 GOLDD analyser: Thermo Scientific Winchester, UK)  
310 held in a test stand (SmartStand, Thermo Scientific, Winchester, UK) (Reidinger *et al.*,  
311 2012).

312

313 Since April 2014, we have carried out regular sampling campaigns to investigate  
314 treatment effects on bulk soil properties (e.g., chemistry, nutrient availability) and  
315 processes (e.g., enzyme activities). Soil samples comprise 8-10 cores (0-10 cm deep, 1  
316 cm wide) per plot. Analyses for soil chemistry, microbial and enzyme activity are  
317 conducted using fresh soil samples; molecular analyses (qPCR and MiSeq Illumina  
318 high-throughput sequencing) are carried out on DNA extracted from frozen samples,



319 using the PowerSoil® kit (MoBio). Results of soil and microbial analyses will be  
320 presented in a subsequent paper.

321

322

### 323 **Statistical analysis**

324

325 All analyses were carried out using linear models in R (Version 3.2.4, R Core Team,  
326 2016). Shelter effects on PAR and air temperature were evaluated for month-long  
327 periods in summer (November 2014) and winter (August 2014), to compare  
328 differences between AMB (sheltered) control plots and outside (unsheltered) control  
329 plots. Data from all 48 sheltered plots were used to evaluate rainfall treatment effects  
330 on plant biomass. Data were first inspected for homogeneity of variances and  
331 normality of errors and, where necessary, log, box-cox or arc-sine transformation was  
332 carried out prior to analyses (Crawley, 2012). Treatment effects were evaluated by  
333 first fitting the full model (rainfall treatment, herbivore addition and their interactions)  
334 and then model simplification was undertaken by removing non-significant terms.  
335 When neither the interaction between rainfall treatment and herbivore addition, nor  
336 herbivore addition on its own were significant ( $P < 0.10$ ), herbivore-added plots were  
337 retained in the analysis to assess rainfall treatment effects. When overall treatment  
338 effects were significant, Tukey's HSD *post-hoc* tests were used to determine  
339 significance between treatment levels; results were considered significant if  $P < 0.05$ .

340

341 Soil moisture data (27 November 2013 to 25 November 2014) obtained from  
342 automatic sensors were averaged per week and the effects of rainfall treatment were  
343 evaluated with a repeated-measures linear mixed-effects model (lme in the nlme

344 package (Pinheiro *et al.*, 2016)) with plot nested within treatment as a random effect.  
345 In order to test for the effect of root herbivore addition, generalized linear mixed  
346 models were constructed with the lmer() function in the lme4 package (Bates *et al.*,  
347 2015), and Chi square ( $\chi^2$ ) values between models with and without the herbivore  
348 interaction were compared (Faraway, 2006). *Post-hoc* comparisons were performed  
349 with glht() in the multcomp package with a ‘Benjamini–Hochberg’ correction  
350 (Hothorn *et al.*, 2008).

351

352 The effect of watering treatment on aboveground invertebrate abundance was assessed  
353 using linear models on square-root transformed abundance data. Watering and  
354 herbivore addition treatments were included in the model as independent variables  
355 along with scaled plot biomass, given the documented effect of underlying plant  
356 structure on sampling efficiency (Facey & Torode, 2016). Effects of root herbivore  
357 addition on the presence/abundance of scarabs in the soil were analyzed with a zero-  
358 inflated-poisson model in the *pcsl* package, and model significance evaluated using a  
359 likelihood ratio (lr) test (Jackman, 2015).

360

361

## 362 **Results and Discussion**

363

### 364 *Shelter effects on microclimate*

365

366 Differences in air temperature between unsheltered and sheltered plots varied diurnally  
367 and between seasons (Table 2). On average (24 hour mean), sheltered plots were 0.04  
368 °C warmer than unsheltered ones, representing non-significant daytime cooling and

369 nighttime warming associated with shelter roofs; this phenomenon is well known from  
370 previous studies using permanently installed shelter infrastructure (Fay *et al.*, 2000;  
371 Beier *et al.*, 2004; Vogel *et al.*, 2013). Whilst temperature was only minimally affected  
372 by the presence of shelter roofs, effects on PAR were more substantial. On average,  
373 PAR was significantly lower under shelters than in outside plots (-15.9%;  $F_{1,2}=145.3$ ,  
374  $P<0.01$ ). Interception losses averaged 17.4% during summer months ( $F_{1,2}=139.5$ ,  
375  $P<0.01$ ) and 13.1% in winter ( $F_{1,2}=198.9$ ,  $P<0.01$ ). This is directly comparable to light  
376 interception values reported for similar studies in Germany (15%, Vogel *et al.*, 2013)  
377 and the USA (21%, Fay *et al.*, 2000) where, like ours, shelter roofs cover the entire  
378 plot area. Lower levels of PAR interception have been associated with shelter  
379 infrastructure where roofs cover a smaller proportion of the plot area. For example,  
380 Gherardi & Sala (2013) report reductions of just 3% and 6% for shelters covering 50%  
381 and 80% of the plots, respectively, while Yahdjian & Sala (2002) found a 10%  
382 reduction in PAR associated with roofs covering 80% of the plot area.

383

384 Light interception is an unavoidable artifact of field experiments involving fixed roofs.  
385 Unless within-shelter PAR is above light-saturation levels for much of the growing  
386 season (e.g. Fay *et al.*, 2000), shelter-induced reductions in PAR are likely to have  
387 implications for photosynthesis and, depending on other resource constraints,  
388 potentially also productivity. Whilst we only measured PAR, it is worth noting that  
389 other shelter-associated changes in spectral characteristics can also influence other  
390 photosensitive ecosystem processes. For example, Vogel *et al.* (2013) attributed  
391 differences in litter decomposition rates and plant metabolic profiles to contrasting  
392 levels of UV radiation associated with shelter roofs in a recent rainfall manipulation  
393 experiment, advocating for the need to include roofed controls in shelter-based studies.

394

395 Outside plots had slightly higher soil water content (SWC) compared to sheltered  
396 AMB plots (Table 3), although differences were not statistically significant ( $\chi^2=0.254$ ,  
397  $df= 1$ ,  $p=0.614$ ). Given the link between canopy transpiration rates and SWC (Patrick  
398 *et al.*, 2014), these differences may be due to slightly higher transpirational water loss  
399 associated with greater vegetation biomass in AMB compared to OP (see below). A  
400 second possible explanation for these differences could be the method for water  
401 delivery to plots. The relatively small droplet size of water applied via sprinklers  
402 increases the chance of both spray drift and higher levels of canopy interception (and  
403 subsequent evaporation) (Moss & Green, 1983), both of which could result in lower  
404 SWC for a given water application, compared to natural rainfall.

405

406 SWC within 25 cm of the edge of RA, RF and SD plots was typically 0-0.5 % higher  
407 than in the centre of the plot. Immediately after heavy ambient rainfall episodes,  
408 differences of up to 2.8% were noted, but overall differences in SWC between the  
409 centre and outside 25 cm of the plot area were small. The biggest differences were  
410 observed in SD plots, following a large rainfall event during the period of total rainfall  
411 exclusion, when within-plot SWC was particularly low. At this time, average SWC  
412 was 23.9% outside of these shelters, while values within SD plots ranged from 2.5% in  
413 the plot centre, to 3.3% and 6.3% at distances of 50 cm and 25 cm from the outer edge  
414 of the plots, respectively. In the context of ambient rainfall incursion, we estimate the  
415 size of the edge effect to be approximately 25 cm. This is directly comparable with  
416 values reported for similar shelters elsewhere (e.g. 20 cm; Gherardi & Sala, 2013), and  
417 confirms that the combination of roof interception, impermeable root barrier and a

418 well-drained, sandy soil provide effective hydrological isolation of our experimental  
419 plots under all but the wettest/windiest conditions.

420

#### 421 *Shelter effects on plant productivity*

422

423 The differences in SWC, air temperature and PAR between AMB and OP were  
424 associated with modest differences in ANPP. Growing season ANPP was 10.8%  
425 higher, and cool season ANPP was 29.7% higher in AMB compared to OP (Figure 2),  
426 although neither of these differences were statistically significant. The larger shelter  
427 effects on cool season productivity were driven by a significantly greater accumulation  
428 of dead plant material in AMB plots (+51%;  $F_{1,22}=7.87$ ,  $P<0.001$ ). Although shelter  
429 impacts on ANPP were not statistically significant, the biological relevance of 10-30%  
430 differences in productivity is arguably high and emphasises the need to compare  
431 treatment effects to sheltered controls (AMB). The importance of controlling for  
432 shelter artifacts has been raised in rainfall manipulation studies elsewhere, with shelter  
433 infrastructure associated with altered NPP, decomposition and carbon fluxes (Fay *et*  
434 *al.*, 2000; Vogel *et al.*, 2013). Based on information on how shelters modify the  
435 microclimate in our study, and associated biological responses, all rainfall and  
436 herbivore treatment effects are evaluated against sheltered AMB plots, with  
437 unsheltered plots used to provide a context for interpreting these effects.

438

#### 439 *Treatment effects and seasonal patterns in soil water content*

440

441 Ambient rainfall at the site for the 12-month period from June 2013 to May 2014 was  
442 597 mm, lower than the 30 year mean of 806 mm. During the first year of the

443 experiment, summer rainfall was particularly low, with less than half the long-term  
444 seasonal average falling in the local area. Temporal trends in SWC are illustrated in  
445 Figure 3. Treatment differences reflect both the timing of ambient rainfall and that of  
446 imposed treatments with, for example, the three-weekly periodicity of the RF  
447 treatment, and the summer-long water withholding in the SD treatments, clearly  
448 reflected in soil moisture patterns.

449

450 Table 3 summarises overall and seasonal treatment effects on SWC for the first 12  
451 months of the experiment. The biggest differences were seen during the summer  
452 (December-February), corresponding to the period of maximum plant growth and the  
453 timing of the SD treatment. There was a significant overall effect of rainfall treatment  
454 on SWC but no effects of herbivore addition, nor an interaction between the two  
455 treatments. *Post-hoc* analyses revealed that moisture levels were higher in AMB  
456 compared to RA plots; RF experienced greater variation in soil moisture, with periods  
457 where SWC was higher and others where it was lower than the other treatments,  
458 during the 21-day watering cycle. The lowest seasonal mean SWCs were associated  
459 with different treatments in different seasons; in winter and spring RF plots had the  
460 driest soils, while in autumn SD had the lowest SWC.

461

462 Annual mean SWC was consistent between all reduced rainfall treatments (RA, RF  
463 and SD) and clearly demonstrates that contrasting rainfall regimes can result in similar  
464 long-term mean SWC, despite highly contrasting patterns both within- and between-  
465 seasons. Increasing rainfall variability (i.e. longer inter-pulse intervals) has been  
466 associated with increased (or decreased) mean SWC, depending on background  
467 climatic conditions and soil type (Zeppel *et al.*, 2014). Under mesic conditions,

468 reducing the frequency of rainfall events (with no change in total rainfall amount) has  
469 been found to lower mean SWC (Harper *et al.*, 2005; Fay *et al.*, 2011), but in arid  
470 systems similar reductions in frequency can actually increase mean SWC, particularly  
471 in deeper soil horizons (Heisler-White *et al.*, 2008, 2009). With a long-term mean  
472 rainfall of 806 mm for the local area, SWC in the RF treatment in our study parallels  
473 that at other mesic sites and highlights the importance of changes in the pattern, as  
474 well as the amount of rainfall for ecosystem hydrology under climate change.

475

476 Unlike field-based rainfall manipulations elsewhere (Fay *et al.*, 2000; Gherardi &  
477 Sala, 2013), differences in seasonal means (Table 3) and temporal patterns (Figure 3)  
478 in SWC between AMB and IA treatments at our site were minimal. This likely reflects  
479 greater transpirational water loss associated with higher plant biomass in IA, and the  
480 high drainage capacity and relatively low soil water-holding capacity (Atwell *et al.*,  
481 1999) of our sandy soils, compared to other studies (e.g. silty clay loam; Fay *et al.*,  
482 2000). It also emphasizes that impacts of future shifts in rainfall regime will be  
483 contingent not only on the nature of the change, but will also depend on the climate  
484 context and soil conditions at a given site.

485

#### 486 ***Early vegetation responses to rainfall and root herbivore treatments***

487

488 Total ANPP in the first growing season (October 13-April 14) was significantly  
489 affected by rainfall treatment ( $F_{4,43}=7.70$ ,  $P=9.03e^{-05}$ ), but there was no effect of  
490 herbivore addition, nor interactions between rainfall and herbivore treatments at this  
491 time. *Post-hoc* comparisons reveal that rainfall effects on ANPP were driven primarily  
492 by a significant reduction (-62.3%,  $P=0.0004$ ) in biomass in SD plots ( $168.4 \pm 46.2$  g

493  $\text{m}^{-2}$ ) compared to AMB ( $446.6 \pm 49.4 \text{ g m}^{-2}$ , Figure 4a). ANPP in IA and RA  
494 treatments were not significantly different from AMB, but there was a clear gradient in  
495 productivity, increasing from  $370.9 (\pm 35.8) \text{ g m}^{-2}$  in RA to  $556.3 (\pm 74.7) \text{ g m}^{-2}$  in IA.  
496 This represents a positive linear relationship between ANPP and water inputs for these  
497 treatments, despite the absence of a clear relationship with mean SWC. ANPP in RF  
498 plots was similar to AMB, despite a somewhat higher mean SWC in RF plots.  
499  
500 Treatment effects on live (green) harvested biomass in April were very similar to those  
501 for total aboveground productivity, with a significant overall effect of rainfall ( $F_{4,43} =$   
502  $6.20, P=0.0005$ ) but not herbivore addition, nor interactions between the two  
503 treatments (Figure 4b). The amount of dead plant material harvested at the end of the  
504 growing season was fairly consistent across plots, with no significant treatment effects  
505 (Figure 4c). However, the ratio of live to dead material differed significantly  
506 ( $F_{4,43}=3.76, P=0.0104$ ) between contrasting rainfall regimes, with dead material  
507 representing 17.8 % of total aboveground biomass in AMB plots, but 58.8 % in SD  
508 plots (Figure 4d).  
509  
510 Taken together, these early data indicate that the total amount of growing season  
511 rainfall is a more important determinant of vegetation productivity at our site than the  
512 frequency of those inputs. Close relationships between rainfall amount and plant  
513 growth are well established (Sala *et al.*, 1988, Hsu *et al.*, 2012; Southon *et al.*, 2012).  
514 However, the lack of biomass response to altered rainfall frequency contrasts with  
515 recent studies that report negative impacts on species productivity, cover and  
516 nutritional quality (Walter *et al.*, 2012; Jones *et al.*, 2016), as well as greater impacts  
517 on ecosystem processes, than reducing total rainfall amount in both mesic (Heisler-



518 White *et al.*, 2009; Fay *et al.*, 2011) and (semi-) arid grasslands (Heisler-White *et al.*,  
519 2008, Miranda *et al.*, 2009). In our study, plant community resistance to altered  
520 rainfall frequency may reflect the high variability in rainfall; coefficients of variation  
521 in seasonal rainfall are naturally high (particularly during spring) at our site compared  
522 to other sites (e.g. Walther *et al.*, 2012) and it is likely that the vegetation has adapted  
523 to historically high levels of rainfall variability. The potential for changes in plant  
524 community composition to buffer changes in ecosystem functioning under more  
525 variable rainfall conditions (Fry *et al.*, 2014b; Gherardi & Sala, 2015) may also  
526 explain the lack of biomass response to RF treatment in our study, and will be a  
527 subject for future investigation.

528  
529 Cool-season (April-October) ANPP and live biomass were not affected by either  
530 rainfall or herbivore addition treatments, or their interactions (Figure 5). Treatment  
531 effects on dead biomass were only significant for rainfall ( $F_{4,43}=3.329$ ,  $P=0.018$ ), with  
532 more dead plant material in RF (+32.1%,  $P=0.017$ ) than AMB at this time. Although  
533 not statistically significant, there was nearly twice as much live plant material in SD  
534 plots in the October harvest as in AMB ( $P=0.096$ ), demonstrating very rapid  
535 vegetation recovery once the summer-long drought was released. This, together with  
536 levels of cool-season productivity in all water-manipulated treatments that were higher  
537 than AMB plots, implies a high degree of climate resilience at our site. The ability for  
538 water-stressed ecosystems to recover is likely associated with rapid recovery of  
539 formerly dominant species, or compensatory growth by other (previously sub-ordinate  
540 or newly recruited) species within these plots. Previous rainfall manipulation studies  
541 have shown contrasting rates of recovery, with evidence of both rapid return to pre-  
542 drought levels of ANPP (Hoover *et al.*, 2014) and legacy effects persisting for many

543 years (Haddad *et al.*, 2002, Sala *et al.*, 2012). Shifts in plant community composition  
544 represent a key mechanism by which physiologically-driven decline in NPP under  
545 drought can be offset (Hoover *et al.*, 2014, Gherardi & Sala, 2015). Compositional  
546 change will, therefore, be closely monitored at our site over the next 3-5 years to  
547 establish the relationship between diversity, community-weighted functional traits and  
548 both resistance and resilience to rainfall change.

549

550 The absence of effects of root herbivore addition on plant productivity responses is not  
551 surprising, given the timing of additions (December 2013 and February/March 2014)  
552 in relation to the first growing season (October 2013-April 2014). Furthermore, given  
553 scarab preferences for grazing on more nutritious grass species (e.g. C<sub>3</sub> species;  
554 Johnson *et al.*, 2014), shifts in community composition may be more likely than  
555 impacts on plot-level productivity. Other studies (e.g. Schallhart *et al.*, 2012) report  
556 root herbivore-associated plant community change, and this may become more  
557 apparent in our study over time.

558

### 559 *Invertebrate responses*

560

561 Root herbivore treated plots contained significantly higher abundances of root-feeding  
562 insects (mostly scarabs) than those that were not inoculated ( $23.3 \text{ m}^{-2} \pm 9.9$  (0-20 cm depth)  
563 and ( $5.6 \text{ m}^{-2} \pm 2.7$  (0-20 cm depth), respectively) (Log-likelihood<sub>5</sub> = -39.6, P = 0.0052).

564

565 Preliminary results from the aboveground invertebrate sampling campaigns found that  
566 invertebrate abundance was not significantly influenced by the imposed rainfall  
567 regimes or root herbivore treatment (Table 4). However, this lack of response in the

568 invertebrate community may change as more data become available from subsequent  
569 sampling campaigns. In particular, we may expect invertebrate abundance above  
570 ground to be negatively affected by the reductions in plant material occurring when the  
571 SD treatment is imposed (December to March).

572

573 No effects of altered precipitation were observed on terms of the abundances of  
574 nematodes, nematode trophic group or microarthropods after more than 1.5 years'  
575 climate manipulation (i.e. April 2015; Nielsen *et al.*, In Press). However, there were  
576 subtle, significant changes in nematode feeding guild composition and diversity in SD  
577 plots, suggesting that nematodes are sensitive to extreme events in this grassland  
578 (Nielsen *et al.*, In Press). Similar results have been observed in other studies (e.g.  
579 Cesarz *et al.*, 2015). These responses will be investigated in depth later in the  
580 experiment, to determine if belowground invertebrate responses are amplified or  
581 ameliorated over time.

582

583 A number of plant chemical characteristics have been measured, but here we focus on  
584 silicon (Si) concentrations because grasses typically accumulate high levels of Si and  
585 this has been shown to increase their resistance to both abiotic (e.g. drought) and biotic  
586 (e.g. herbivory) stress (Epstein, 1999, Cooke and Leishman, 2011). In particular, Si  
587 has been demonstrated to be an inducible defense against aboveground herbivores  
588 (Massey *et al.*, 2007). We found similar patterns of induction in two of our three  
589 sampled grasses, *Cynodon dactylon* and *Eragrostis curvula*, in response to  
590 belowground herbivore addition (Figure 6). To our knowledge, this is the first example  
591 of belowground herbivores inducing this defense in grasses. Future work will report

592 whether this effect persists and whether rainfall treatments moderate the induction of  
593 this important plant defense.

594

595

## 596 **Conclusion**

597

598 This paper introduced a new experimental platform that, uniquely, combines multi-  
599 level rainfall manipulation with contrasting levels of root herbivory. Early data clearly  
600 identify the importance of shelter controls in rainfall manipulation experiments of this  
601 type, in order to assess potential shelter artifacts that may otherwise obscure treatment  
602 effects. This SE Australian grassland exhibited relatively high resistance of NPP to  
603 changes in the size and frequency of rainfall inputs, except under extreme summer  
604 drought (SD). The rapid recovery of NPP in SD plots after ambient rainfall inputs  
605 were resumed indicates that low ecosystem resistance to climate extremes is not  
606 necessarily associated with low functional resilience. This may reflect adaptation of  
607 the plant community to the naturally high variability in rainfall that can occur both  
608 between- and within- years in Australia, with annual inputs at our site varying by as  
609 much as 66% below and 114% above the long-term mean. The absence of a  
610 productivity response to herbivore addition may be a consequence of the timing of this  
611 treatment in relation to the first growing season, compensatory growth by affected  
612 plant species and/or changes in plant community composition. This research platform  
613 will allow ongoing monitoring of ecological responses to novel combinations of  
614 abiotic and biotic stresses, and identification of mechanisms underlying observed  
615 above- and belowground responses.

616

617 One of the biggest challenges in ecosystem ecology today is to improve our  
618 understanding of the mechanisms by which plant physiological and morphological  
619 responses to climate change affect interactions within- and between- trophic levels,  
620 and ecological feedbacks (Van der Putten *et al.*, 2010). The DRI-Grass experimental  
621 platform provides the opportunity to gain important new insight into how ecological  
622 interactions are affected by changing rainfall regimes and, specifically, how  
623 belowground herbivory modifies grassland resistance and resilience to climate  
624 extremes.

625

626

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635

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647

648

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892 belowground insect herbivory: A meta-analysis. *Oecologia* 169, 441–452.  
893 doi:10.1007/s00442-011-2210-y.
- 894  
895

896 Table 1. Soil properties at the DRI-Grass field site. \*Exchangeable nutrient  
 897 concentrations obtained using ion exchange membranes (Plant Root Simulators®);  
 898 values measured at 0-10 cm depth.

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 900

Soil property	Value (units)
Texture	84.4 % sand 7.4 % silt 9.2 % clay
SOM content	2.4 %
pH	6.4
Total N	0.011 mg g <sup>-1</sup>
Total P	0.0016 mg g <sup>-1</sup>
*Exchangeable NO <sub>3</sub>	17.1 µg cm <sup>-2</sup> 90 days <sup>-1</sup>
*Exchangeable NH <sub>4</sub>	3.6 µg cm <sup>-2</sup> 90 days <sup>-1</sup>
*Exchangeable PO <sub>4</sub>	1.55 µg cm <sup>-2</sup> 90 days <sup>-1</sup>
Bulk density	1.66 g cm <sup>-3</sup>
C:N ratio	12.98
Water holding capacity	0.21 ml ml <sup>-1</sup>

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In review

904 Table 2. Shelter effects on canopy air temperature and PAR.  
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		Air temperature (°C)			PAR (mean daily mol m <sup>-2</sup> )		
		Outside	Shelter	Diff (°C)	Outside	Shelter	Diff (%)
Overall	24 hour	15.73	15.77	+0.04	-	-	-
	Daylight hours	19.43	19.24	-0.19	34.98	29.43	-15.9%
	Night time	12.04	12.30	+0.26	-	-	-
Summer (Nov)	24 hour	20.46	20.48	+0.02	-	-	-
	Daylight hours	23.70	23.55	-0.15	41.54	34.30	-17.4%
	Night time	17.23	17.42	+0.19	-	-	-
Winter (Aug)	24 hour	11.15	11.21	+0.06	-	-	-
	Daylight hours	15.30	15.08	-0.22	27.41	23.80	-13.1%
	Night time	7.01	7.35	+0.34	-	-	-

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In review

909  
 910 Table 3. Mean seasonal and annual volumetric soil water content (SWC, %) and  
 911 seasonal rainfall (mm), 2013-2014. Values in brackets represent  $\pm 1$  SE. Rainfall  
 912 treatment effects on SWC are evaluated for all sheltered plots (i.e. excluding  
 913 unsheltered control plots). Ambient rainfall means and coefficients of variation (CoV)  
 914 also summarized by season, for the past 30 years (1982-2012).

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Treatment	Winter	Spring	Summer	Autumn	Annual
Ambient (sheltered)	14.0 (0.49) a	10.3 (0.45) a	10.0 (0.32) a	13.0 (0.34) a	11.8 (0.22) a
Reduced amount	12.2 (0.46) b	9.2 (0.48) a	8.6 (0.20) a	10.0 (0.23) b	9.9 (0.19) b
Increased amount	13.0 (0.51) a	10.2 (0.55) a	9.8 (0.43) a	13.0 (0.43) a	11.4 (0.25) ab
Reduced frequency	11.1 (0.43) b	7.7 (0.40) a	8.6 (0.45) a	12.5 (0.40) a	10.0 (0.23) ab
Summer drought	13.8 (0.50) a	10.9 (0.51) a	8.7 (0.30) a	7.3 (0.03) b	10.0 (0.22) ab
Treatment effects (df=1,4)	$\chi^2=23.5,$ P=0.0001	$\chi^2=7.85,$ P=0.097	$\chi^2=8.06,$ P=0.089	$\chi^2=21.4,$ P=0.0003	$\chi^2=15.3,$ P=0.009
Outside plots (unsheltered)	14.3 (0.55)	11.4 (0.55)	10.5 (0.36)	15.3 (0.45)	12.8 (0.26)
<b>Ambient rainfall (mm)</b>					
06/2013-05/2014	80.4	230.9	124.7	160.6	596.7
30-year mean	137.6	182.4	280.7	205.6	806.3
30-year CoV	77.3%	41.4%	43.4%	60.8%	26.1%

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919 Table 4. Mean total aboveground invertebrate abundances (individuals) from the first

920 sampling campaign (October 2013). Values in brackets represent  $\pm 1$  SE.

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Rainfall treatment	Mean total aboveground invertebrate abundance	
	Sticky traps	Vacuum samples
Ambient	216.8 (20.2)	133.8 (36.8)
Increased Amount	209.3 (18.9)	225.5 (61.9)
Reduced Amount	233.4 (19.0)	165.8 (43.4)
Reduced Frequency	227.8 (15.2)	396.5 (143.0)
Summer Drought	237.5 (27.0)	230.0 (59.7)
Rainfall	$F_{4, 39} = 0.430$ $P = 0.786$	$F_{4, 39} = 9.70$ $P = 0.435$
Herbivore	$F_{1, 39} = 1.506$ $P = 0.227$	$F_{1, 39} = 0.297$ $P = 0.589$
Rainfall*Herbivore	$F_{2, 39} = 0.302$ $P = 0.741$	$F_{2, 39} = 0.015$ $P = 0.989$

In review



923 **Figure legends**

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925

926 Figure 1. Schematic of DRI-Grass rainout shelter design.

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928 Figure 2. Harvested plant biomass in sheltered ambient and outside (unsheltered) plots

929 in a) April 2014 (growing season) and b) October 2014 (cool season).

930

931 Figure 3. Temporal trends in soil water content, by treatment from November 2013 to

932 November 2014.

933

934 Figure 4. Rainfall treatment effects on growing season biomass (April 2014 harvest):

935 a) Aboveground NPP (October-April), b) live biomass, c) dead biomass, d) live:dead

936 biomass ratio. Values are means +/- 1SE.

937

938 Figure 5. Rainfall treatment effects on cool season biomass (October 2014 harvest): a)

939 Aboveground NPP (April-October), b) live biomass, c) dead biomass, d) live:dead

940 biomass ratio. Values are means +/- 1SE.

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942 Figure 6. Effects of root herbivore addition treatment on foliar silicon concentrations

943 in *Cynodon dactylon* and *Eragrostis curvula*.

Figure 1.JPEG

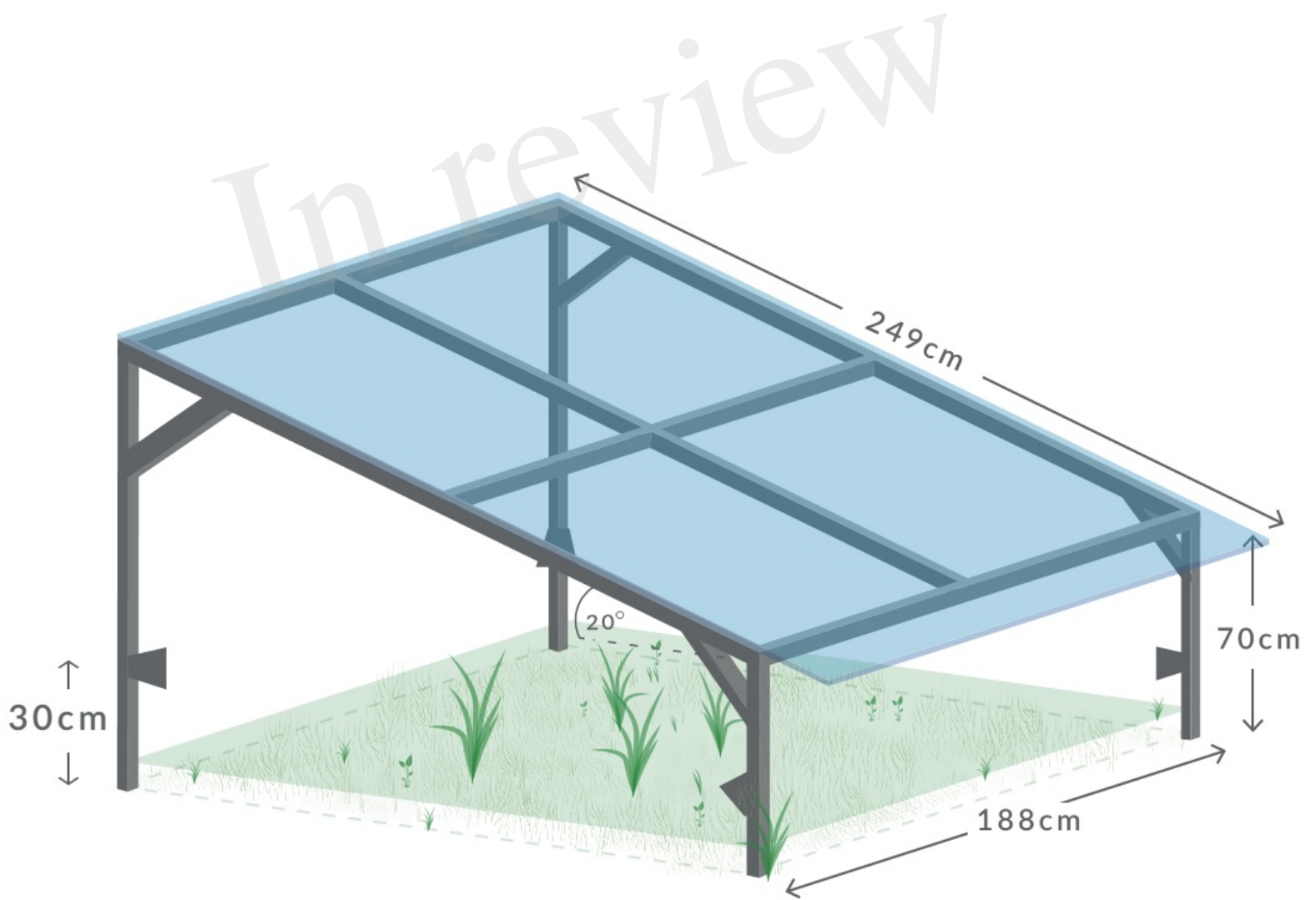


Figure 2.TIFF

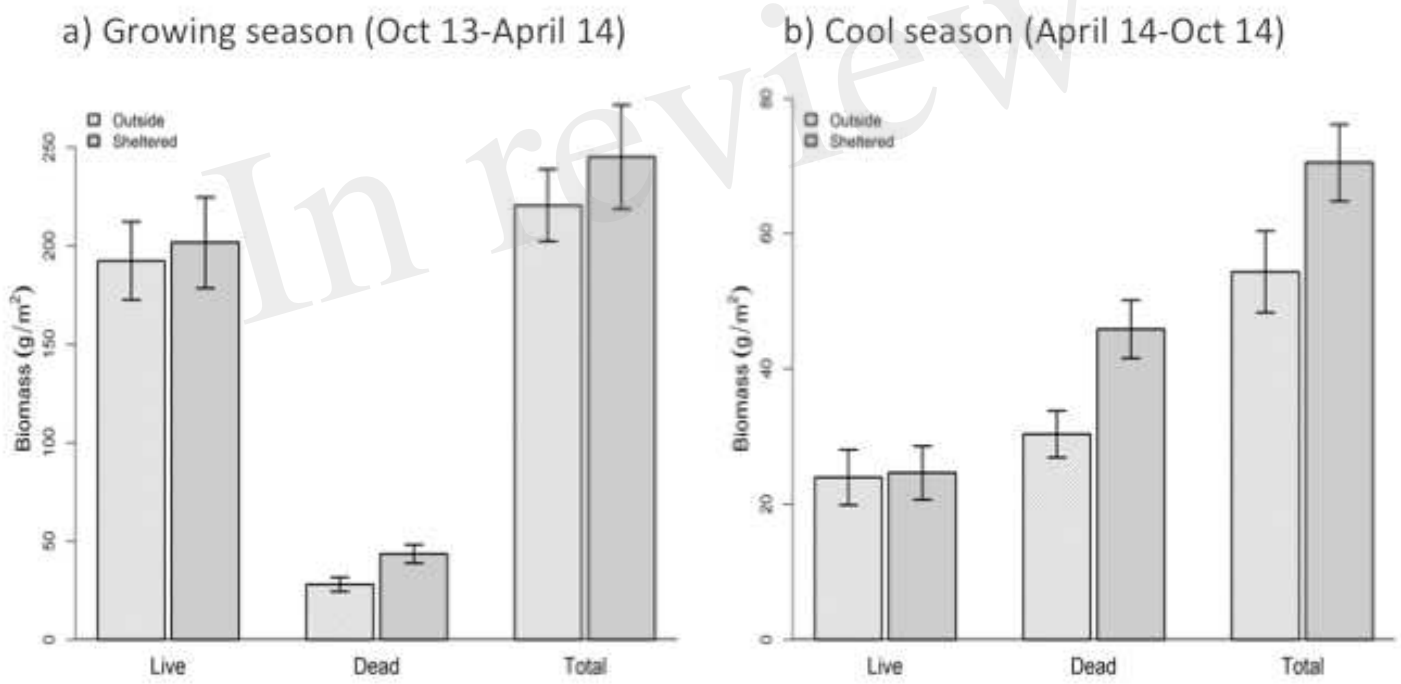


Figure 3.TIFF

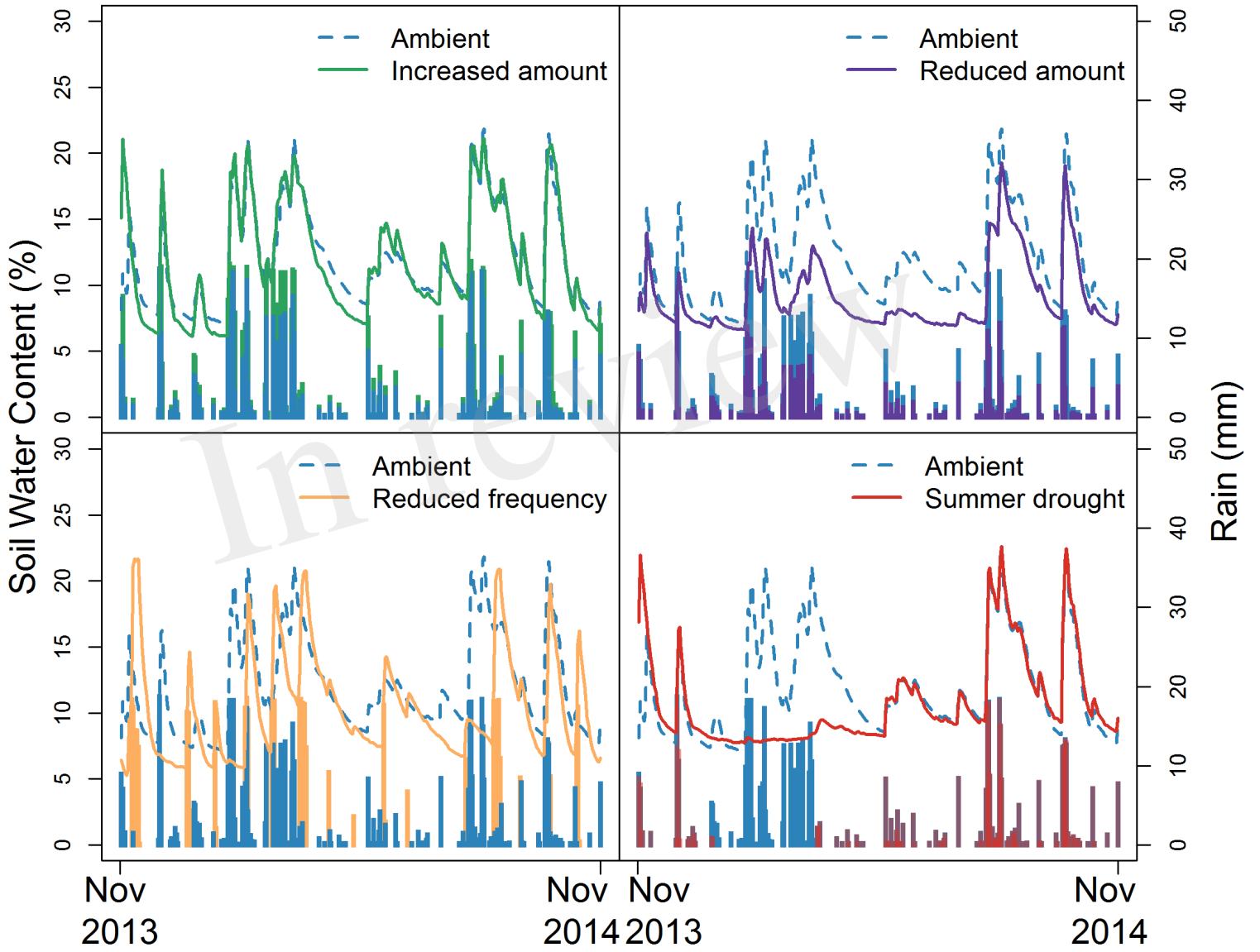


Figure 4.TIFF

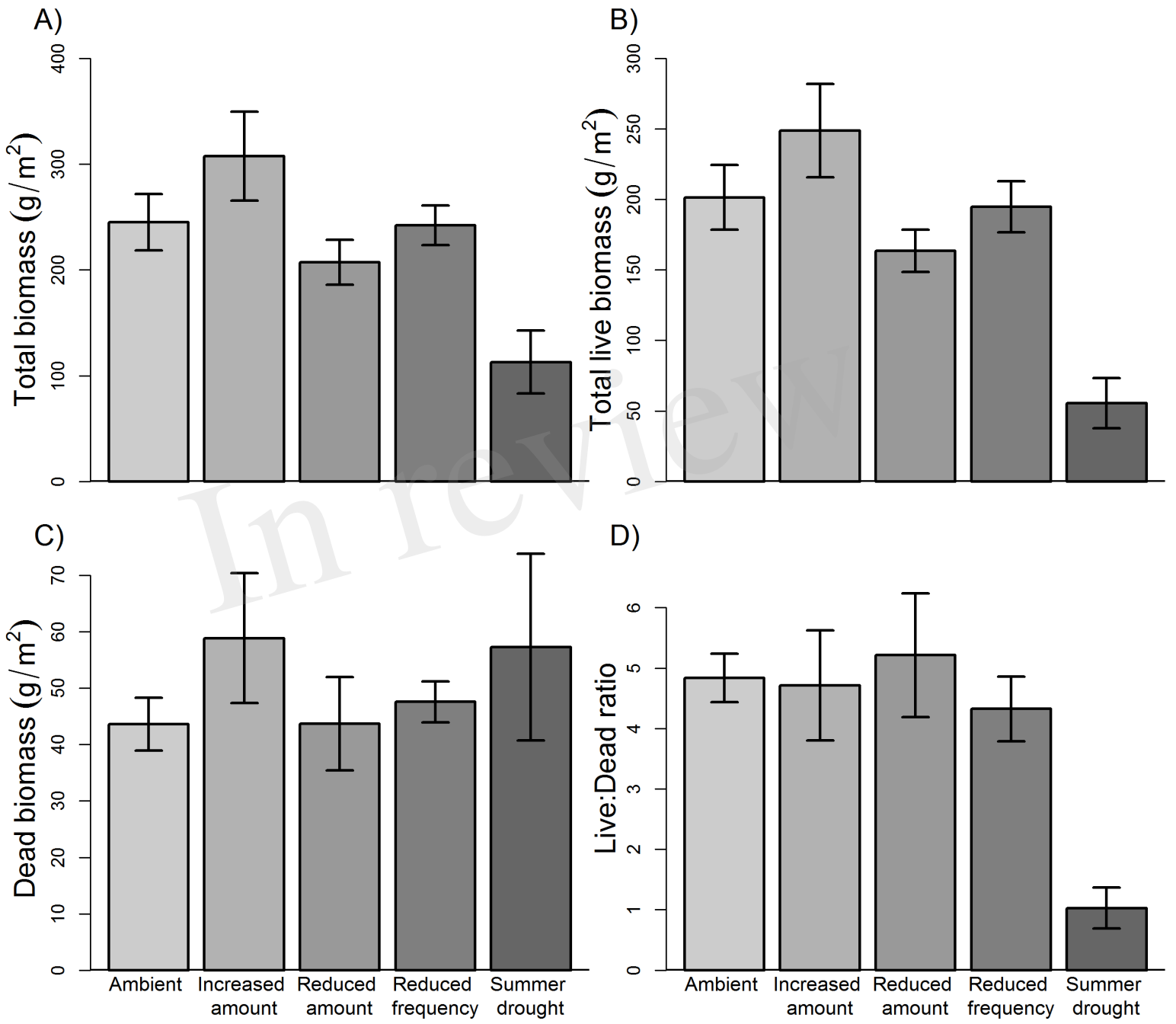


Figure 5.TIFF

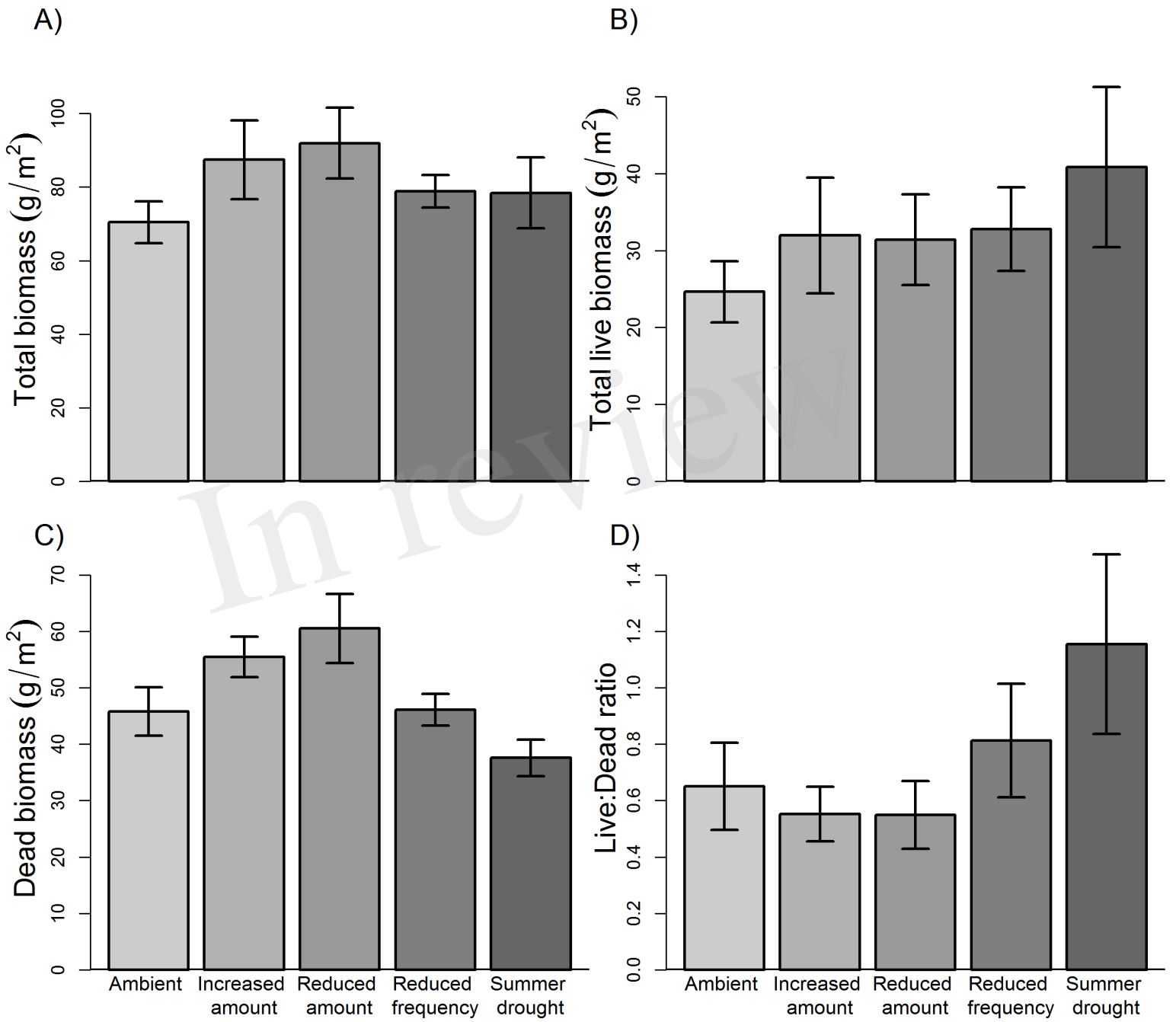


Figure 6.TIFF

