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1 **The dynamics of designed plant communities of rosette forming forbs for use in supra-**
2 **urban drainage swales.**

3 **James Hitchmough and Markus Wagner**

4

5 **1 Introduction**

6 Over the past decade there has been a substantial change in attitudes to how wet, seasonally
7 anaerobic soil is perceived in designed, urban landscapes (Dunnett and Clayden, 2007). This
8 is due to the desire to collect and infiltrate rainwater into soil as opposed to using
9 conventional pipe drainage systems, to reduce flooding further down the catchment (Wheater
10 and Evans, 2009). Equally important has been the shift from an agricultural-horticultural
11 perspective in which waterlogged soil represents a loss of potential productivity that requires
12 rectification (Spoor, 2004), to an ecological perspective which sees these conditions as an
13 opportunity to support additional biodiversity (Kazemi et al., 2011) and create aesthetic
14 experiences for people (Dunnett and Hitchmough, 2004). These ecological approaches to wet
15 soil are long established in rural or peri-urban landscapes but are relatively new to the
16 mainstream politic of intensely urban places (Hill, 2009).

17 Climate change has further increased interest in these approaches particularly where
18 precipitation is predicted to become either more frequent or intense, or both, as in the case of
19 North Western Britain (Murphy et al., 2009). Embracing seasonally anaerobic soil will
20 require new types of plant communities to be designed. To date, much of the thinking on wet
21 plant communities has been undertaken by drainage engineers for SUDS (Sustainable Urban
22 Drainage schemes) that are rural in character or in location (CIRIA, 2007), and not closely
23 scrutinised by the public. Such schemes have often relied, to a greater or lesser degree, on

24 natural colonisation by native wetland plants, a sensible, sustainable approach in these
25 contexts.

26

27 In more intensely designed urban environments, these approaches are not always tenable.

28 There is a greater need to recognise how landscape scale, content, human aesthetic aspiration
29 (Gobster, et al., 2007) and the resources available for landscape design and management
30 might interact to create demand for a plurality of vegetation types and experiences.

31 Urban design practice in cities such as Portland, Oregon (Dunnett and Clayden, 2007),
32 programmes to disconnect public, private and domestic roof water from conventional
33 drainage systems (Emanuel and Godwin, 2010), plus the work of designer-researchers such
34 as Kircher (2004) demonstrate a more culturally nuanced approach to planting design for
35 anaerobic soil.

36 This vegetation might range from species-poor, spontaneous communities of
37 competitive tall forbs and grasses, through to more intensely managed systems that use
38 uncompetitive, typically stress-tolerating (*sensu* Grime 2001) species. The latter might be
39 natives or aliens that are strongly valued within the urban garden culture of a particular
40 country often because of their long flowering season, very early, or very late, or dramatic
41 flowering display. Nassauer's (1995) cues to care notions are very appropriate to these
42 situations, where people are confronted with new, radically different designed environments,
43 potentially very close to where they live.

44 Landscape architects will be more interested in using non-native species in parts of
45 the world where the native flora is numerically depauperate, and the garden culture highly
46 developed, as for example in Western Europe, rather than in countries such as the USA and
47 China, where large land surface area, plus high species richness allows much larger numbers

48 of species to be considered “politically native” (Hitchmough, 2011). An important factor
49 determining what plant species are appropriate where, will be degree of connectivity between
50 the parts of the drainage system, plus the reproductive strategies (Grime, 2001) and potential
51 performance (Daehler, 2003) of the plant species. Where connectivity with drainage
52 networks beyond the site is high, non-native species characterized by a high reproductive
53 capacity are likely to be inappropriate. On the other hand, where connectivity is low, highly
54 attractive exotic species of low reproductive fecundity (sexual and asexual) may also be
55 appropriate.

56 Irrespective of whether species used are native or exotic, their architecture-
57 morphology and response to stress and disturbance are critical considerations for the design
58 process. These factors provide designers with the capacity to; i) create plant communities in
59 which the tendency for competitive dominance by a few species can be diminished, ii)
60 produce visually and structurally diverse, long-flowering and highly detailed plant
61 communities that are attractive to ordinary people (as opposed to only those with specialised,
62 learnt ecological knowledge) (Gobster et al., 2007) as well as to native invertebrates and
63 other wildlife (Schwab et al., 2002).

64 One architectural-morphological type that satisfies many of these requirements is the
65 low-stature rosette-forming forb, with a leaf-less inflorescence. In contrast to species with tall
66 leafy stems (the predominant architecture in productive wetland ecosystems), low-stature
67 rosette formers have greatly reduced capacity to outcompete their neighbours for light, and
68 thus are less likely to lead to monocultural communities. This brake on dominance allows
69 more diversity to be designed in, and potentially retained in the longer term through
70 management.

71 This in turn facilitates greater seasonal change, particularly in terms of the number and
72 duration of flowering events that can be generated per m². Attractive flowering displays are

73 key to gaining broad public support for designed urban vegetation (Özgüner and Kendle,
74 2006; Lindemann-Matthies and Bose, 2007; Lindemann-Matthies et al. 2010). Even when
75 composed of completely randomly placed plants, communities of rosette-forming forbs
76 appear “tidy”, because of their relatively ordered structure and lower standing biomass (Jay
77 and Stolte, 2011). Such structurally-complex vegetation is also valuable for delivering
78 ecosystem services to native wildlife and in particular, invertebrates (Morris, 2000).

79 Low-stature rosette forbs' capacity to persist is normally restricted to unproductive
80 habitats where insufficient nutrients, water (dry habitats) or oxygen (wet habitats) combined
81 with disturbance factors such as grazing or fire inhibit the formation of a tall leafy sward
82 dominated by more competitive species (Grime, 2001). Hence, designed communities of
83 rosette forbs are, at the level of the component species, less likely to be stable and persistent
84 than taller leafy stem species, except where potential productivity of the soil is low or
85 management is used to prevent their competitive exclusion. In many parts of the world,
86 diverse plant communities containing stress-tolerant rosette-forming forbs of low stature are
87 increasingly rare (Smart et al., 2003; Stevens et al., 2006). The ecology of rosette forb
88 dominated communities is therefore a significant issue for conservation and restoration
89 ecology, as well as landscape architecture.

90 In this study, the emphasis was placed on *Primula*, an almost entirely rosette forming
91 genus of some 430 species, that are typically highly attractive to urban people (Richards
92 2002). Many species of the Sino-Himalayan *Primula* Sections *Proliferae* and *Sikkimenses*
93 were introduced into cultivation between 1870 and 1920 and are now important, culturally
94 valued garden plants in cool oceanic climates (Richards, 2002). These species' natural
95 habitats are C3-grasslands along drainage lines, usually on poorly-drained substrates
96 (Handel-Mazzettii, 1929), and grazed by wild and domestic ungulates which selectively

97 avoid *Primula* species (Shaheen et al., 2011), thus facilitating their persistence through
98 defoliation of potential dominants.

99 Many of these *Primula* species are relatively competitive in soils that are wet during
100 spring to summer, but under drier conditions they are rapidly outcompeted by, for example,
101 common European meadow grasses (Hitchmough and Innes, 2007). Seedlings are small, and
102 relatively slow-growing, but moderately tolerant of shading, and relatively unpalatable to
103 molluscs. *Primula* species vary considerably in longevity, (Richards, 2002), but high levels
104 of seed production facilitate persistence of populations even in species that are relatively
105 short-lived as individuals, with seed rain localised around adult plants.

106 For urban vegetation to be more sustainable, it is essential that the design of such
107 vegetation is informed by management.. Designed native vegetation nearly always represents
108 an extant plant community with known management requirements. North American mesic
109 prairie, for example, is burnt in March at 2-4 year intervals, with the biomass cut and
110 removed from the site in other years (Packard and Mutel, 1997). European mesic hay
111 meadow is cut and the biomass removed in summer, often followed by aftermath grazing in
112 autumn and spring (Crofts and Jefferson, 1999). With designed vegetation not closely based
113 on native reference communities, applying extensive nature-conservation based management
114 techniques is more problematic, as the species used (whether native or exotic) are drawn from
115 a broader range of semi-natural communities characterized by different forms of
116 management. Such vegetation requires a more creative approach to management, based on
117 assessment of factors such as plant architecture, phenology and site productivity (Luken,
118 1990; Koningen, 2004). Given this, it is feasible to design sustainable vegetation,
119 irrespective of the origin of the constituent species, that can be managed extensively and
120 sustainably, by techniques originally devised for nature conservation (Hitchmough, 2009).

121 This study looks at the effect of soil wetness and time of canopy defoliation, on
122 competition within sown communities of rosette-forming forbs of both Western European
123 species and non-native species dominated by Sino-Himalayan *Primula*. The overall aim of
124 the research was to investigate the viability of this plant community for use in seasonally
125 anaerobic situations such as SUDs in urban landscapes. The research questions were as
126 follows:

- 127 • Once established at high densities, can communities of rosette-forming forbs resist
128 invasion from common native plant species with other growth morphologies?
- 129 • Does increasing soil wetness during the summer growing season, which was achieved
130 in this study by additional irrigation, increase or decrease persistence, seedling
131 regeneration, individual plant size or community diversity?
- 132 • Does the date of cutting and removal of the community biomass affect plant
133 persistence, regeneration, individual plant size and community diversity?
- 134 • To what extent do the effects of cutting date and of soil wetness level depend on each
135 other, i.e. do they interact?

136

137 **2 Materials and Methods**

138 **2.1 Field site and experimental set-up**

139 An attempt was made to utilise an actual SUDs scheme to undertake the research, but none of
140 the available sites were suitable. Consequently the study was located at the Royal
141 Horticultural Society's Garden at Harlow Carr in Harrogate, North Yorkshire (53°59 N;
142 1°34' W; altitude: 150 m) in a species poor mown grassland subject to severe winter, spring
143 and autumn water-logging. The grassland was typical of gang-mown urban greenspace in

144 Northern Britain, and was dominated by ubiquitous wet tolerant species such as *Agrostis*
145 *stolonifera*, *Holcus lanatus*, *Ranunculus repens*, and various *Juncus* spp. suppressed by regular
146 mowing. The experimental site was adjacent to a woodland and sloped gently (< 5%) to the
147 east, and received upslope surface run-off. The site shared many of the characteristics of
148 SUDS schemes, being saturated post rainfall even in summer, and then gradually drying prior
149 to the next rainfall event. Annual mean rainfall in Harrogate for the period 1992-2006 was
150 793 mm with a minimum of 575 mm and a maximum of 1134 mm. The site has an oceanic
151 climate, for 2005-9, mean annual temperature was 9.9°C, with a July mean temperature of
152 16.4°C (Knaresborough and Scotton Weather Station Data Archive, 2012). The clay loam
153 soil (pH 5.5) was moderately productive, and in the previous year, when unmown, had
154 supported a standing biomass of approximately 500g dry matter / m² (Hitchmough, 2009).
155 The main herbivores associated with the site were slugs which were abundant given the wet
156 conditions.

157 The randomised plot experiment involved twelve 2.4 m x 4.8 m experimental plots,
158 six of which were irrigated and six non-irrigated. The aim of irrigation was to apply enough
159 water to approximate to mean Western Scotland, May-August precipitation (Dunstaffnage,
160 1971-2001 mean, 370 mm) (Met. Office, 2012) to which many Asian *Primula* species of wet
161 habitats are demonstrably well-fitted (Richards, 2002). Approximately 8 mm of water was
162 applied to all irrigated plots at weekly intervals from May to August via drip irrigation. Each
163 plot was split into two subplots on the basis of management treatment, one cut in September
164 and one cut in November.

165 Experimental plots were marked out in Spring 2004. In each of the two subplots per
166 plots, four permanent 750mm x 750mm quadrats were marked out in a regular 2 × 2 grid. To
167 prevent extant vegetation in the grassland from eliminating sown species, the former was
168 eliminated through the application of a glyphosate herbicide. In practice, SUDS schemes

169 often involve deep excavation into existing, *in-situ*, inverted or transported subsoils from
170 which vegetative plants and weed seed banks are absent, and where this is the case, initial
171 weed control inputs are often unnecessary. In July 2004, the dead turf was stripped off to a
172 depth of 75 mm. The experimental plots were surfaced with a 75 mm layer of mixed (50:50
173 by volume) composted green waste/deep-subsoil to provide a weed seed free sowing mulch
174 that effectively prevented weed seed emergence from the underlying soil. . The markedly
175 reduced competition this technique provides in the first year greatly improves both
176 establishment and longer-term persistence of sown species (Hitchmough et al., 2008).

177 All plots were sown on August 5th 2004 with a seed mix containing 15 *Primula*
178 species (see Table 1) at a rate of 100 seeds per m². *Primula rosea* ‘Gigas’ was sown at 150
179 seeds per m² on account of its very small seed and anticipated lower establishment. Seed
180 weights of individual species are given in Hitchmough et al. (2011). Where possible, fresh
181 seed produced in summer 2004 was used, as this is typically non-dormant in many *Primula*
182 species (Baskin and Baskin, 1998). Species not available as fresh seed were purchased from
183 Jelitto Perennial Seeds (Schwarmstedt, Germany). Species with known physiological seed
184 dormancy were purchased as “Gold Nugget” seed, a proprietary Jelitto product pre-treated to
185 remove dormancy. After sowing, all plots were rolled and covered with 20 mm mesh-size
186 Jute erosion matting. The first *Primula* seedlings emerged approximately 14 days post
187 sowing.

188 A further six wet grassland species, four native and two non-native (see Table 1) were
189 over-sown on all plots in December 2004 at 100 seeds per m². The seeds of several of these
190 species are physiologically dormant and require a period of chilling prior to germination (see
191 Wagner et al. (2011) for *S. pratensis*), and the December sowing ensured that this
192 requirement was met. *Persicaria milletii* and *Succisa pratensis* were sown to provide
193 flowers in July and August, to extend the flowering period. In addition to meeting chilling

194 requirements for germination, staggered sowing was used because previous research had
195 shown that some of these species may gain dominance when sown at the same time as the
196 *Primula* species. Weed invasion was largely restricted by the sowing mulch, but a few large
197 weed seedlings emerging in 2005 were removed by hand-pulling..

198 **2.2 Assessment**

199 A baseline count of the number of plants of each sown species in the four 750 mm x 750 mm
200 permanent quadrats was carried out in April 2006. Prior to this it was very difficult to
201 distinguish reliably between *Primula* species. A second count in June 2006 dealt with species
202 emerging from dormancy very late in the year (*P. alpicola* and *P. sikkimensis*) and three
203 closely related species (*P. bulleyana*, *P. beesiana*, and *P. burmanica*) that could only be
204 reliably identified when in flower. Counts were repeated in 2007, and again in 2009.

205 Total cover of sown species, unsown species and bare ground was assessed in April
206 2009. In September 2009, above-ground biomass was harvested in the permanent quadrats of
207 five of the six replicate plots of each irrigation treatment and sorted into *Primula* spp.,
208 unsown graminoids (i.e. grasses and rushes), and forbs other than *Primula*; in the latter
209 category, sown and unsown forbs were lumped together. Before weighing, biomass was dried
210 in a drying cabinet at 80°C. In April 2009, a visual assessment of the relative density of
211 newly emerged *Primula* seedlings was carried out in all permanent quadrats, using an ordinal
212 scale ranging from 1 to 3. Subplots were then sorted on these scales in relation to cover
213 values and other variables and 16 permanent quadrats chosen for an assessment of seedling
214 regeneration and survival. In each of these quadrats, three small 100 mm x 100 mm quadrats
215 were placed at random to determine the number of *Primula* seedlings present in April 2009.
216 To determine seedling survival, a further *Primula* seedling count was carried out in exactly
217 the same three small quadrat positions in September 2009.

218

219 **2.3 Data analysis**

220 To avoid pseudo-replication, prior to statistical analyses, plant count data from the four
221 permanent quadrats per subplot, were summed, and biomass and cover data were averaged
222 across the four permanent quadrats).

223 With the exception of ordination analyses which were carried out using CANOCO,
224 version 4.5 (Ter Braak & Šmilauer, 2002), all statistical analyses were carried out using R,
225 version 2.12.2 (R Development Core Team, 2011).

226 To characterize sown community diversity, based on plant counts carried out in 2006,
227 2007 and 2009, we calculated species density and Smith-Wilson evenness (E_{var}) values
228 (Smith and Wilson, 1996) based on a reference area of 2.25m² (i.e. the total area of the four
229 permanent quadrats in each subplot). Prior to statistical analyses, counts of individuals and
230 of species were square-root transformed to improve distributional properties.

231 To analyse treatment and year effects on community diversity and on the numbers of
232 individuals of sown species individually and pooled together, we carried out repeated-
233 measures ANOVAs using R's 'car' package (Fox, 2011). In these analyses, experimental
234 plots represented subjects, irrigation represented a between-subjects factor, and year and
235 cutting date represented within-subjects factors. Greenhouse-Geisser correction was used to
236 adjust P-values associated with main and interaction effects of 'Year' for possible violations
237 of sphericity.

238 To analyse both general trends in community composition as well as cumulative
239 effects due to experimental treatments, we carried out two ordination analyses. As we were
240 interested in treatment effects on relative species composition, species count data was
241 standardised by sample norm for these analyses (Lepš & Šmilauer, 2003). In the light of the

242 short vegetation gradients revealed by an initial Detrended Correspondence Analysis (all axes
243 < 1.7), partial Redundancy Analysis was our method of choice. Analysis 1 focused on general
244 trends over time irrespective of treatment by including Year, coded as ranging from 0 (for
245 2006) to 3 (for 2009), as explanatory variable. To control for location-specific differences
246 and for treatment-driven trends, subplot ID, coded as twenty-four 0/1 dummy variables, and
247 interactions of treatments with time (Irrigation \times Year and Cutting Date \times Year) were
248 included as covariables. Analysis 2 specifically tested the effects of additional irrigation and
249 of differences in cutting date on vegetation development by including treatment interactions
250 with time as explanatory variables, and Year and subplot ID as covariables. Overall
251 significance was assessed by Monte Carlo tests based on the reduced model (9999
252 permutations), with permutations restricted to take into account experimental design (Lepš
253 and Šmilauer, 2003). To assist interpretation in terms of variance explained, we carried out a
254 third analysis, including Year, Cutting Date \times Year and Irrigation \times Year as explanatory
255 variables, and subplot ID as covariable.

256 To analyse treatment effects on 2009 standing biomass of *Primula* spp., other forbs,
257 and graminoid species, we carried out split-plot ANOVAs using R's aov function. Diagnostic
258 plots confirmed that the requirements of constancy of variance and of normality of errors
259 were met without data transformation.

260 To investigate direct relationships between numbers of *Primula* seedlings in April
261 2009, equivalent numbers in September 2009, percentage seedling survival, calculated as
262 ratio between September numbers and April numbers, and, percentage cover of bare ground,
263 sown species, and unsown species, we carried out Spearman rank correlations, significance
264 being evaluated with two-sided tests ($N = 16$).

265

266 **3 Results**

267 **3.1 Density of sown species at the onset of experimental assessments (2006)**

268 Mean density of sown plants in 2006 ranged from 90 to 100 plants per m² across the
269 experiment (Fig. 1A). Individual species differed greatly in initial density. Fig. 2 shows plant
270 densities for all three years, with species ordered on the basis of 2006 plant density, with the
271 Y-axis scale changing accordingly. *Primula pulverulenta*, the species that established best
272 (Fig. 2A), had densities in 2006 of about 20 plants per m². Many other species showed
273 moderate establishment with between 3 and 10 plants per m² (Fig. 2, panels D-M), while
274 eight species established very poorly, with densities of 2 plants per m² or lower (Fig.2, panels
275 N-U).

276

277 **3.2 Changes in plant density between 2006 and 2009**

278 Overall densities of sown plants, as revealed by repeated-measures ANOVA, showed a
279 strongly significant decline ($P < 0.001$) from about 90 to 100 plants per m² in 2006 to about
280 50 plants per m² in 2009 (Table 1, Fig. 1A). There were however huge species-level
281 differences in the extent to which this took place (Fig. 2), resulting in a significant shift in
282 relative community composition over time, as illustrated by a significant effect of Year in the
283 partial RDA analysis that had Year as explanatory variable (Analysis 1; Table 2, Fig. 3). This
284 shift was mostly towards four species that maintained more or less stable plant densities
285 throughout the experiment, including two native species (*Primula vulgaris* and *Succisa*
286 *pratensis*; Fig. 2 panels K and L) and two non-native species (*P. pulverulenta* and *P. rosea*;
287 Fig. 2, panels A and D), all as a result pointing in the same direction as the Year arrow in the
288 ordination biplot (Fig. 3), indicating an increase over time in the relative proportion of these
289 species within the sown community. Accordingly, due to the relative stability of their

290 populations over time these four species were characterised by a non-significant Year effect
291 in their respective repeated-measures analyses of variance (Table 1). Plant numbers of two
292 other species, *Primula burmanica* and *Dodecatheon jeffreyi*, slightly declined over time (Fig.
293 2, panels H and Q), but maintained their overall importance within the sown community, as
294 indicated by the fact that their species arrows in the pRDA biplot (Fig. 3) were at a right
295 angle to the Year arrow. In the case of *D. jeffreyi*, this decline was too weak to result in a
296 significant Year effect in the repeated-measures ANOVA (Table 1). Of the remaining species
297 that successfully established at the beginning of the study (i.e. those species with plant
298 densities in 2006 regularly exceeding one plant per m²), five (*P. bulleyana*, *P. denticulata*, *P.*
299 *poissonii*, *P. prolifera*, and *P. veris*) markedly declined throughout the study but were
300 nonetheless still present in substantial numbers in 2009. By contrast, *P. beesiana* and *P.*
301 *japonica* had almost disappeared from the plots, and *C. pratensis* and *P. chionantha* were
302 extinct by 2009. Similarly, most of the species that initially established very poorly were no
303 longer present in the experimental plots in 2009, with the exception of *Ranunculus acris* and
304 *D. jeffreyi*.

305

306 **3.3 Management effects on the sown community, aboveground biomass, and average** 307 **size of *Primula* plants**

308 The partial RDA that included Cutting Date \times Year and Irrigation \times Year as explanatory
309 variables (Analysis 2) remained non-significant ($P = 0.559$; Table 2), i.e. even after three
310 years, there was still no detectable influence of experimental management treatments on
311 community composition. Similarly, when analysing the performance of individual species by
312 means of repeated-measures ANOVAs, a significant interaction effect between Cutting Date
313 and Year was found in only one species, *P. poissonii* ($P = 0.032$; Table 1), and not in a single
314 species was there a significant Irrigation \times Year interaction. While there were significant

315 main treatment effects in a few species (Cutting date: *P. burmanica*, *P. japonica*, *P. prolifera*;
316 Irrigation: *R. acris*) these appear to be largely due to the fact that initial densities in spring
317 2006, before treatments started, already markedly differed by chance between plots assigned
318 to different treatments. In only one of these species, *P. burmanica*, a slight tendency may
319 exist to experience a slightly weaker numerical decline in plots cut in November, but even in
320 this instance, the interaction between Cutting Date and Year falls short of significance
321 ($P = 0.109$; see Table 1). The weight of evidence suggests that species composition was not
322 affected by three years of experimental management.

323 Species density of sown species declined markedly and highly significantly over time
324 ($P < 0.001$; Table 1; Fig. 1B). Sown communities in different years also differed with respect
325 to evenness ($P = 0.038$; Table 1) but in this case differences were rather subtle, with Fig. 1C
326 suggesting a slightly lower evenness in 2009 than in previous years. In both instances,
327 treatment interactions with Year were non-significant.

328 Analyses of data from the summer 2009 biomass harvest suggest that biomass of
329 *Primula* spp. (Fig. 4A) was increased both by additional irrigation ($P = 0.011$; Table 3) and
330 by the later cut in November (Split-plot ANOVA, $P = 0.030$; Table 3). Similarly, as numbers
331 of *Primula* plants were fairly constant between treatments, this meant that average size of
332 *Primula* plants was affected in the exact same manner (Fig. 4B, Table 3). By contrast,
333 graminoid standing biomass and non-*Primula* forb biomass were not affected by management
334 treatments (Fig. 4C,D, Table 3).

335

336 **3.4 *Primula* seedling regeneration in relation to vegetation structure**

337 We did not find any evidence from Spearman correlations for *Primula* seedling survival,
338 calculated as the ratio between seedling numbers in September 2009 and numbers in April

339 2009, to be affected by cover of sown species, cover of unsown species or by percent cover
340 of bare ground in spring (Table 4). Similarly, neither were seedling numbers in April or
341 September affected by any of these parameters. As there also was no correlation between
342 survival percentage and seedling numbers in April, a density-dependent regulation of
343 seedling mortality can be ruled out. However, a pronounced and highly significant ($r_s = 0.70$;
344 $P = 0.002$) correlation between seedling numbers in spring and autumn of the same year
345 underlines that establishment strongly depends on successful seedling emergence in spring.

346

347 **4 Discussions**

348 **4.1 Seedling density at the outset of the study**

349 Whilst the focus of this study was response to longer-term management rather than
350 establishment, to inform application to practice, some comment is made on the latter. Due to
351 the difficulties in identifying *Primula* seedlings to species level, the first census count was
352 not carried out until spring 2006. The densities recorded in 2006 therefore represent
353 percentage emergence in autumn 2004 and spring 2005 minus losses, e.g. due to predation or
354 competition.

355 While not formally assessed, seedling emergence appeared to have been particularly
356 low in the eight species with the lowest 2006 densities (Figure 2). Two of these, *Persicaria*
357 *milettii* and *Primula sikkimensis*, were sown as fresh seed. The remaining non-native species
358 were sown as Jelitto seed with minimum laboratory germination of 70%. Native species
359 were obtained from the UK native wildflower seed industry in which, in common with
360 equivalents in other countries, there are no minimum germination standards, and seed quality
361 thus can be highly variable (Ryan et al., 2008). Three of the eight poorly emerging species
362 (*L. flos-cuculi*, *P. milettii*, and *R. acris*) were oversown in November 2004 after other species

363 had emerged, and could not be incorporated into the soil by raking, and this may have
364 reduced emergence. This did not, however, limit emergence of the two other oversown
365 species, *Cardamine pratensis* and *Succisa pratensis*.

366

367 By 2006 most *Primula* species had established between 3 and 10 plants per m², including *P.*
368 *rosea*, the species sown at 150 seed per m². *P. pulverulenta* had established an average of
369 about 20 plants per m² from a sown density of 100 seeds per m². This species was sown from
370 fresh seed and this may have maximised its establishment (Hitchmough et al., 2011). It
371 represented 20-25% of all sown plants in the 2006 census, and as the most vigorous of the
372 *Primula* species used, exerted a disproportionate effect on the developing community.

373

374 **4.2 Changes in plant density and community diversity over time**

375 As is normal in designed sown vegetation (Hitchmough et al., 2008), density of individual
376 sown plants declined by approximately half between 2006 and 2009. Thinning due to
377 competition for light both within the sown and unsown plants is likely to have played a
378 dominant role. This interpretation is supported by relatively high observed levels of standing
379 biomass of approximately 500 g per m² in our experimental plots (Wilson and Tilman, 1991).
380 Other sources of mortality for sown plants may have been herbivory (del-Val and Crawley,
381 2004), and potentially poor adaptation to the prevailing site conditions. The observed decline
382 in the density of individual plants may also provide a simple explanation for the marked
383 decline in species diversity, as fewer individuals may almost inadvertently have resulted in
384 the representation of fewer species per unit area.

385 The main agent of thinning appears to be *P. pulverulenta*, the species present at the
386 highest density. This species had the fastest growth and largest foliage rosette of the *Primula*

387 species, making it a superior competitor for light (Grime 2001). The combination of rapid
388 growth and being present at high density led to *P. pulverulenta* dominating the community
389 (Schwinning and Weiner, 1998). The positive aspect of the dominance of *P. pulverulenta*
390 was high resistance to invasion from outside the community.

391 The main unsown invaders of the experimental plots (in decreasing order of standing
392 biomass) were *Juncus* spp., *Agrostis stolonifera*, *Holcus lanatus* and *Ranunculus repens*: all
393 common in the wet grasslands surrounding the experiment. These species typically colonise
394 aggressively by seed or vegetative means (Grime et al., 2007). *Juncus* spp. appeared to
395 establish particularly well because their upright growth habit allowed their culms to thrust
396 through seasonal gaps in the dense *Primula* canopy.

397 The annual counts strongly suggested that *Primula* spp. were regenerating from self-
398 sown seed and this was confirmed by the seedling counts in April and September 2009.
399 Seedling mortality is however high, with seedling numbers in the September count averaging
400 46 % of those in the April. Survival showed no correlation with factors that were anticipated
401 to be important such as quadrat cover of sown or unsown species, or bare ground in spring.
402 However, as there was considerable variation in survival, ranging from 3 % to 74 % among
403 the 16 monitored permanent quadrats, it seems likely that successful recruitment is
404 nonetheless dependent on highly spatially and temporally variable factors, such as density of
405 shade or the pattern and intensity of mollusc predation. Although *Primula* spp. are
406 unpalatable as adults (Shaheen et al., 2011) they are consumed by molluscs as small seedlings
407 (Hitchmough, personal observation).

408

409 **4.3 Performance of individual species across the study.**

410 Four species, *P. pulverulenta*, *P. rosea* 'Gigas', *P. vulgaris*, and *S. pratensis* maintained
411 stable populations across the four years of the study. Two further species, *D. jeffreyi* and *P.*
412 *burmanica* suffered comparatively small losses. These six species have very little in common
413 that would distinguish them from the group of less successful species, and thus, different
414 factors may be responsible for their comparatively good performance. Two are native to
415 Western Europe (*P. vulgaris* and *S. pratensis*), one is native to high altitude wet grassland in
416 Western North America (*D. jeffreyi*), and three are from wet grassland in the Sino Himalayan
417 region (*P. burmanica*, *P. pulverulenta* and *P. rosea*). These species can be split into two
418 groups on rosette size. *Dodecatheon jeffreyi*, *P. burmanica*, *P. pulverulenta* and *S. pratensis*,
419 are tall-statured (typically > 250 mm tall) with large rosettes (> 250 mm wide), and thus can
420 compete effectively for light and space. *Primula rosea* and *P. vulgaris*, on the other hand, are
421 small-statured (< 100 mm tall) with small rosettes (< 150 mm wide). However, as both are
422 vernal species that flower in March and April before the foliage of the taller species is fully
423 developed, they can tolerate being "over-canopied" by the foliage of other species later in the
424 season. In the British Isles, *P. vulgaris* is typically a woodland species in southern lowland
425 areas, whereas in northern and western areas it tends to be more common in more open,
426 grassy habitats (Jacquemyn et al., 2009). *Primula rosea* occurs in species rich Western
427 Himalayan grasslands where it is subject to shading in summer by taller forbs and grasses. An
428 evergreen rosette might be anticipated to be advantageous in terms of competition for light
429 across the year, but of the successful species only *Succisa pratensis* is fully evergreen.
430 Several *Primula* spp. that showed a pronounced decline in our study are also evergreen, such
431 as *P. poissonii*, *P. prolifera* and *P. secundiflora*. It thus appears that a larger leaf canopy or
432 the capacity to withstand heavy shading may be more important for persistence than duration
433 of leaf retention.

434 Species persistence in competitive herbaceous vegetation is strongly and often
435 unpredictably affected by local factors such as fitness to climate, soil moisture and herbivory
436 regimes (Hitchmough 2009). Species with only moderate shade tolerance and a large part of
437 their foliage flush with the ground, in rosettes or other spatial arrangements, included *Lychnis*
438 *flos-cuculi*, *Ranunculus acris*, *Persicaria miletii*, *P. alpicola*, *P. poissonii*, *P. secundiflora*, *P.*
439 *sikkimensis*, and *P. sinopurpurea*. The dominant *P. pulverulenta* probably reined in these
440 species in the same way as community dominants in semi-natural are known to determine the
441 abundance and fitness of subordinate species (Grime 2001). To achieve a favourable balance
442 at the establishment stage of designed plantings between potential dominants and subordinate
443 species, designers need to rank species in terms of their relative growth rate and canopy size,
444 and adjust sowing densities in favour of the subordinates.

445 Palatability of adults and seedlings to slugs was an important factor behind the poor
446 performance of some species; *Cardamine* was “eaten out” long before 2009. *Primula*
447 *japonica* was observed to be the most palatable of the *Primula* species, followed by *P.*
448 *beesiana*, which appears to be substantially more palatable than its close relatives, *P.*
449 *bulleyana* and *P. burmanica*. Vegetation design in moist oceanic climates needs to be aware
450 of the impact of this factor on plant sustainability (Hitchmough and Wagner, 2011).

451 *Primula veris*, a common native species, may have declined because the site was too
452 wet, although its shade intolerance may also have played some role (Brys and Jacquemyn,
453 2009). The non-native and otherwise robust *P. denticulata*, a species of drier, Himalayan
454 meadows, (Shaheen, et al. 2011), may also have been maladapted to the wet site conditions.
455 It seems likely that both species would persist on the drier and less productive shoulders of
456 actual SUDS swales.

457

458 **4.4 Management effects on the sown community**

459 Neither additional irrigation, nor timing of the annual cut had a significant effect on the total
460 number of individuals of sown plant species present in the experiment. This suggests that the
461 soil was wet enough without supplementary irrigation, and that cutting in September still
462 allowed sufficient photosynthetic productivity to allow the sown species to survive over the
463 five years of the study. Many of the non-European *Primula* species in the study are associated
464 with grazed wet grasslands (Handel-Mazzettii, 1929) rather than summer cut meadows. They
465 are generally relatively unpalatable to herbivores (Shaheen et al. 2012), and not subject to
466 defoliation prior to the onset of winter, and as such would have been anticipated to be
467 intolerant of early autumn cutting. By contrast, several of the native European forbs, such as
468 *Succisa pratensis*, are associated with summer or autumn cut meadows, or enter dormancy in
469 late summer, as in the case of *Ranunculus acris*. An early September cut may have been
470 expected to shift community composition in favour of the native European species, but was
471 not observed.

472 Overall, the general absence of a response of the sown community to the experimental
473 treatments in terms of both composition and diversity might have been expected given the
474 relative similarity in life histories and ecological characteristics among the sown species.
475 Unsown colonists from the surrounding grasslands and in, particular graminoids, showed a
476 different response to *Primula* species.

477 Nonetheless, cutting even earlier in the year, for example in August, could result in
478 greater impacts, as shown by Hitchmough (2009) and, by more strongly affecting tall-statured
479 species, lower the risk to subordinate species of being competitively excluded by dominant
480 species such as *Primula pulverulenta*. This has frequently been observed in semi-natural
481 grassland communities (Grime 2001).

482 Cutting and irrigation did however have a clear visual, and statistically significant
483 effect on both *Primula* standing biomass and mean weight of *Primula* individuals (Table 3,
484 Figure 4). Both were increased by supplementary irrigation and by the later cut in November.
485 In contrast, the standing biomass of non-*Primula* forbs, dominated by *Succisa*, and of
486 colonising graminoids, dominated by *Juncus* spp. and weedy grasses of wet sites, was not
487 significantly affected by irrigation or timing of cutting. Consequently, the ratio of *Primula*
488 biomass to biomass of graminoids, the dominant colonists of the experiment, was highest for
489 irrigated plots that were cut in November. In previous studies with sown, designed
490 herbaceous vegetation (Hitchmough and De La Fleur, 2006), such high biomass ratios were a
491 good indicator of successful long-term performance. Our study thus suggests that the
492 resistance of sown *Primula* meadows to invasion by weedy species may be particularly high
493 on wetter sites cut in November compared to drier sites cut in September.

494 The current study has demonstrated that high-density sowings of individually
495 relatively small rosette-forming forbs on moderately productive moist to wet soils, managed
496 by non selective annual cutting and removal of canopy biomass were markedly resistant to
497 invasion by weedy species over a 5 year period. This resistance was due to the fact that the
498 sowing mulch used prevented weed emergence from the soil seed bank at the initial stage,
499 and that the *Primula* canopy, which fused in late summer 2005, greatly reduced opportunities
500 for colonisation by weedy seedling colonists, thus resulting in a relatively stable vegetation.

501 Individual rosette biomass is also important in terms of flowering display. Most forb
502 species are adapted to start flowering only once a certain size threshold is crossed, and the
503 level of resource investment in flowering is directly proportional to plant size (Zhang and
504 Jiang, 2002). Moreover, such relationships between plant size and flowering, and in particular
505 size thresholds for flowering have also been identified for *Primula* species (e.g. Shimono and
506 Washitani, 2007; Brys et al., 2011). This affects visual (floral) impact of the vegetation,

nectar value to native invertebrates, and the capacity of the *Primula* species to produce seed and establish new seedling recruits. By 2009, November-cut plots were clearly more floriferous than September-cut ones.

4.5 The experimental plant community in relation to landscape architectural practice

One of the most compelling lessons from this study is the importance of what happens at the beginning of the establishment phase for the long-term performance of designed vegetation. The 75mm deep sowing mulch facilitated high emergence and establishment of the sown species whilst preventing the emergence of most weedy species from the underlying soil. This provided the basis for dominance over the next 5 years by species that would not normally be seen as competitive enough to do this. The experiment was set in mown wet grassland in a public garden, surrounded by woodland, and weedy hedgerows-roadsides. Competitive ruderals such as *Ranunculus repens*, *Agrostis stolonifera*, *Holcus lanatus*, as well as tall species such as *Chamaenerion angustifolium*, and *Urtica dioica*, that often colonise designed herbaceous planting from wind blown seed, were present close to the experiment. The very low density of these colonists after five years appears to be due to three factors; i) sowing mulches inhibited establishment in the first growing season, ii) the dense overlapping canopies of the dominant *Primula* species eliminated many seedling colonists that establishing after the first year through shading; iii) the site was very wet for much of the year, reducing the pool of potential colonists to species adapted to anaerobic soils, such as *Juncus* species.

Since this experiment was established in 2004, sowing mulches have been developed by the lead author in commercial landscape practice to engineer a diversity of species-rich herbaceous vegetation types, often on a large scale, throughout Britain (Richardson, 2011). If complex, species-rich, vegetation is to be established on a large scale, for reasons of cost, plus its low carbon credentials (Cameron et al; 2012) sowing seed *in situ* will need to be used

532 more. At the same time, in highly urbanised, politically contested sites, it is imperative that
533 the resulting plant communities are attractive to the public. One of the key factors in this is
534 initial suppression of weed emergence from the soil seed bank.

535 A good example of these processes is the 2012 London Olympic Park, where the lead author
536 (Hopkins and Neal, 2012) successfully established over 10ha of meadows and SUDS swales
537 using sowing mulches. Subsoil is an ideal material for sowing mulches in SUDS swales and
538 rain gardens, as it is low cost and provides excellent germination of sown species. It is also
539 low in nutrients and hence favours the persistence of rosette-forming species as discussed in
540 this paper. The use of jute erosion matting as described in this study is also valuable in
541 practice as it stabilises the surface of sowing mulches reducing “seed wash” in swales prior to
542 emergence and establishment. In many cases establishment can be further facilitated in SUDs
543 by establishing vegetation several months before connecting swales to surface run off
544 drainage systems.

545

546 Although the key experimental aims of the study were to explore biological aspects of the
547 designed community, we were also interested in the visual characteristics of the developing
548 vegetation. All *Primula* species and most other sown species with the exception of *D. jeffreyi*
549 (2007) flowered in 2006. Flowering and leaf phenology of the species are shown in Figure 6.
550 The first species to flower (late March) were *Primula rosea* (cerise pink), *P. denticulata*
551 (mauve, purple, and crimson), *Cardamine pratensis* (pale pink), *P. vulgaris* (cream) and *P.*
552 *veris* (yellow). The second wave of flowers commenced in May with *P. pulverulenta* (cerise-
553 crimson), *L. flos-cuculi* (pink) and *R. acris* (yellow). June was dominated by *Primula*
554 *beesiana* (pink), *P. bulleyana* (yellow-orange), *P. burmanica* (crimson), and *P. prolifera*
555 (yellow), with the last primula to flower generally *P. poissonii* (crimson). Approximately four
556 months of dramatic flowering (see Figure 5) was generated, with *Succisa pratensis* providing

557 lavender blue flowers into September. With the exception of the early spring species, most of
558 the species in the experimental vegetation bore flower at the ends of leafless stems up to
559 900mm tall. This architecture is important in terms of maximising visual drama, creating a
560 “see-through” effect of flowers floating in space, surrounded by the multi-hued blooms of
561 other species. This contrasted with the low, symmetrical rosette leafage providing a sense of
562 neatness and order.

563 Feedback from the visiting public suggested it was the most-talked about aspect of the garden
564 between May and July. The vegetation was also highly attractive to insects foraging for
565 nectar and pollen, such as bees, butterflies, moths and hoverflies, which were present in high
566 densities during the flowering season.

567 As the vegetation developed, the extraordinary flowering displays evident in 2006 and
568 2007 gave way to less dramatic but still attractive displays, as *Primula* density and diversity
569 declined. Whilst species such as *P. pulverulenta*, were clearly able to persist in the longer
570 term, even if these *Primula* were only medium-term ephemerals, to be mixed with
571 structurally similar native species, they would be useful in providing initial drama, that in
572 turn would help build support among local people for supra-urban SUDS.

573 In a Western European context, additional native species that would be compatible
574 with SUDs dominated by forb species with rosette-like, basal leafage would, amongst others,
575 include *Allium schoenoprasum*, *Ajuga reptans*, *Caltha palustris*, *Cruciata laevipes*, *Geum*
576 *rivale*, *Knautia arvensis*, and *Trollius europaeus*. Taller, clump-forming, emergent species
577 not used in the present study, might include *Iris sibirica* and *Euphorbia palustris*. There are
578 also many exotic forbs with similar growth habits associated with wet sites that would be
579 valuable additions to these rosette-like plant communities, including *Geum coccineum*,
580 *Hemerocallis lilioasphodelius*, *Persicaria bistorta* var. *carnea*, and *Polemonium reptans*.

581 Even with careful design, predictability of outcomes in practice will always be limited
582 by site-specific conditions and idiosyncrasies. Thus, when aiming to establish ecologically
583 informed vegetation, the best design strategy is to build in extra capacity to cope with a lack
584 of fitness in individual species, by using a wider range of species in seed and planting mixes
585 (Hitchmough, 2009). Designers of ecologically based landscape vegetation also need to
586 recognise plant traits that are likely to lead to dominance, and to respond by reducing the
587 densities of such species relative to those of less productive species to avoid accelerated
588 extirpation of the latter. The present study illustrates the unintentional consequences for
589 longer-term community development of not doing this. By using identical seed densities for
590 all species but one, without compensating for dominance potential or likely differences in
591 percentage field emergence, subordinate species were at a disadvantage from the outset.

592 Over the five-year period of the experiment, there was no evidence of establishment
593 of non-native sown species outside the treatment blocks. These observations are in
594 agreement with previous experiences of these species in Britain. Despite widespread
595 cultivation, often in rural gardens and close to semi-natural habitats, records of establishment
596 outside of gardens are rare, and largely restricted to *P. florindae* (Preston et al., 2002), under
597 wet conditions the most competitive *Primula* species and not used in this study for this
598 reason. Regeneration of these species is generally restricted to within the managed vegetation
599 type, at levels permitted by the intensity of shading and predation by molluscs.

600

601 **5 Conclusions**

602 In the present study, the most obvious effect of increased soil moisture levels during the
603 summer growing season was to increase *Primula* total and individual biomass, and to
604 enhance the flowering display, but over a five-year period it did not significantly affect

605 retention of sown-species richness. Similarly, the longer photosynthetic window afforded by
606 cutting and biomass removal in November also increased *Primula* total biomass and
607 individual biomass, compared to cutting and removal in September. Observations by the first
608 author indicated that this was particularly marked in those *Primula* species that in general are
609 not subject to summer defoliation in their habitats. There was no evidence from this study of
610 cutting date and supplementary irrigation interacting with one another.

611 Most importantly though, this work has shown that once established at high densities,
612 even on relatively productive moist soil, communities of relatively unproductive rosette-
613 forming forbs can resist invasion by more productive, colonising plant species for at least five
614 years, and probably much longer, under a simple nature conservation form of management,
615 involving annual defoliation in early or late autumn. Critical for achieving persistence and
616 resistance to invasion appears to be establishment of a closed canopy of desirable species by
617 the end of the first growing season, with both weedy unsown species and potentially
618 dominant sown species being limited to low densities. The use of sterile sowing mulches to
619 inhibit weedy species from the soil seed bank and seed mix design to take account of
620 potential differences between species in emergence and potential competitive dominance, are
621 also critical for maximizing success.

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779 Table 1. Results of repeated-measures ANOVAs of plant count data collected in 2006, 2007, and 2009, and of diversity parameters derived from these count
780 data. Significance testing of main and interaction effects involving the within-subjects factor Year are Greenhouse-Geisser-corrected, and correction factors ϵ_1
781 and ϵ_2 are listed alongside with corrected P-values. Significant terms in bold. Names of native species are marked with (N).

Parameter	Intercept		Irrigation (I)		Cutting Date (C)		C × I		Year (Yr)		I × Yr		C × Yr		I × C × Yr		$\epsilon_1(\text{GG})$	$\epsilon_2(\text{GG})$
	F _{1,10}	P	F _{1,10}	P	F _{1,10}	P	F _{1,10}	P	F _{2,20}	P ϵ_1	F _{2,20}	P ϵ_1	F _{2,20}	P ϵ_2	F _{2,20}	P ϵ_2		
Plant counts																		
Pooled sown species	193.73	<0.001	0.03	0.876	2.00	0.188	0.02	0.898	42.85	<0.001	0.18	0.756	0.31	0.670	0.19	0.760	0.690	0.725
<i>Primula alpicola</i>	3.89	0.077	0.06	0.817	0.02	0.884	1.76	0.214	4.11	0.069	0.24	0.638	0.21	0.694	0.76	0.422	0.509	0.588
<i>Primula beesiana</i>	35.15	<0.001	0.00	0.981	0.30	0.597	0.00	0.997	35.18	<0.001	0.58	0.507	0.55	0.577	2.59	0.103	0.672	0.963
<i>Primula bulleyana</i>	65.35	<0.001	0.01	0.916	0.06	0.808	0.43	0.526	19.05	<0.001	0.14	0.858	0.49	0.550	0.14	0.790	0.944	0.673
<i>Primula burmanica</i>	174.73	<0.001	0.01	0.922	21.46	<0.001	0.11	0.749	16.18	<0.001	0.04	0.922	2.49	0.109	0.93	0.412	0.774	0.994
<i>Primula chionantha</i>	18.95	0.001	1.01	0.340	0.05	0.836	0.04	0.852	22.40	<0.001	0.78	0.419	0.39	0.613	0.08	0.862	0.618	0.710
<i>Primula denticulata</i>	20.26	0.001	0.24	0.636	0.01	0.907	0.07	0.804	23.87	<0.001	0.12	0.835	0.74	0.469	0.68	0.493	0.771	0.831
<i>Primula japonica</i>	60.95	<0.001	0.00	0.977	6.08	0.033	1.40	0.264	29.84	<0.001	0.22	0.675	1.59	0.234	1.19	0.320	0.562	0.797
<i>Primula poissonii</i>	159.14	<0.001	0.00	0.946	1.49	0.250	0.23	0.645	38.45	<0.001	0.29	0.653	4.15	0.032	3.03	0.072	0.630	0.986
<i>Primula prolifera</i>	46.52	<0.001	0.07	0.801	7.00	0.024	0.32	0.585	25.10	<0.001	0.77	0.416	1.85	0.198	1.83	0.200	0.579	0.677
<i>Primula pulverulenta</i>	69.79	<0.001	0.15	0.702	1.68	0.224	0.03	0.868	0.02	0.940	0.07	0.876	1.24	0.308	0.10	0.861	0.704	0.803
<i>Primula rosea</i> ‘Gigas’	281.34	<0.001	0.00	0.958	4.62	0.057	0.47	0.510	0.30	0.609	0.82	0.395	1.22	0.306	0.47	0.563	0.535	0.677
<i>Primula secundiflora</i>	16.76	0.002	0.01	0.940	1.57	0.239	1.05	0.329	13.53	0.001	0.07	0.875	1.45	0.260	0.38	0.645	0.694	0.811
<i>Primula sikkimensis</i>	6.50	0.029	0.49	0.502	1.19	0.302	0.26	0.624	7.43	0.019	0.28	0.623	0.33	0.620	0.12	0.787	0.531	0.609
<i>Primula veris</i> (N)	22.39	<0.001	0.01	0.937	0.20	0.663	0.62	0.448	24.52	<0.001	1.39	0.272	0.65	0.527	0.12	0.881	0.824	0.949
<i>Primula vulgaris</i> (N)	33.25	<0.001	0.17	0.686	0.01	0.944	0.12	0.738	2.24	0.153	1.55	0.243	0.03	0.916	0.29	0.662	0.686	0.652
<i>Cardamine pratensis</i> (N)	43.51	<0.001	0.01	0.925	0.57	0.469	0.00	0.970	54.43	<0.001	0.01	0.980	0.65	0.468	0.02	0.940	0.751	0.626
<i>Dodecatheon jeffreyi</i>	14.68	0.003	0.05	0.830	0.07	0.799	0.28	0.610	0.73	0.437	0.52	0.521	0.83	0.428	0.23	0.748	0.614	0.796
<i>Lychnis flos-cuculi</i> (N)	6.77	0.026	0.08	0.778	0.00	0.949	1.12	0.315	4.25	0.044	0.05	0.909	0.15	0.775	1.51	0.250	0.746	0.672
<i>Persicaria milletii</i>	4.40	0.062	0.00	0.982	0.00	0.967	0.00	0.967	2.82	0.087	0.48	0.613	2.06	0.178	0.51	0.516	0.943	0.573
<i>Ranunculus acris</i> (N)	24.21	<0.001	8.19	0.017	0.25	0.627	0.00	0.959	4.67	0.044	3.08	0.097	0.65	0.474	1.83	0.201	0.627	0.653
<i>Succisa pratensis</i> (N)	62.83	<0.001	0.97	0.349	0.29	0.601	0.55	0.475	1.34	0.280	0.48	0.553	0.16	0.810	0.27	0.724	0.664	0.811
Diversity parameters																		
Spp. richness × 2.25 m ²	2256.7	<0.001	0.05	0.834	0.55	0.475	0.02	0.890	37.73	<0.001	2.65	0.096	0.06	0.930	2.11	0.154	0.988	0.890
Evenness (E_{var})	406.35	<0.001	0.00	0.946	0.15	0.706	0.24	0.633	4.68	0.038	3.09	0.091	0.31	0.732	0.77	0.474	0.695	0.981

782 Table 2. Results of partial Reduncancy Analyses (pRDAs) of sown community composition based on
 783 plant count data collected in 2006, 2007, and 2009. Analysis 1 investigates general effects of time
 784 since sowing (Yr), and Analysis 2 investigates trends over time due to experimental irrigation (I) and
 785 cutting date (C), which is a comparison of September vs. November cutting dates. The third analysis
 786 was carried out to aid interpretation of variance terms. Model significance according to Monte Carlo
 787 test based on 9999 permutations. Significant terms in bold. See text for details.

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Analysis	Explanatory variables	Covariables	λ_1	$\Sigma \lambda_{CAN}$	$\Sigma \lambda$	P_{MODEL}
pRDA (= Analysis 1)	Yr	Plot ID; Yr \times C; Yr \times I	0.060	0.060	0.245	< 0.001
pRDA (= Analysis 2)	Yr \times C; Yr \times I	Plot ID; Yr	0.006	0.010	0.195	0.559
pRDA	Yr; Yr \times C; Yr \times I	Plot ID	0.165	0.175	0.360	N/A

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800 Table 3. Results of split-plot ANOVAs of *Primula* mean weight and *Primula*, other forb, and
 801 graminoid standing biomass based on data collected in 2009. Significant terms in bold.

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Source	D.f.	<i>Primula</i> mean weight		<i>Primula</i> standing biomass		Forb standing biomass		Graminoid standing biomass	
		F	P	F	P	F	P	F	P
Error: Block									
Irrigation (I)	1	8.09	0.022	10.69	0.011	0.01	0.921	0.00	0.978
Residuals	8								
Error: Cut Date within Block									
Cut Date (C)	1	6.05	0.039	6.99	0.030	0.20	0.667	0.59	0.464
I × C	1	0.05	0.821	0.5	0.500	2.29	0.168	0.00	0.956
Residuals	8								

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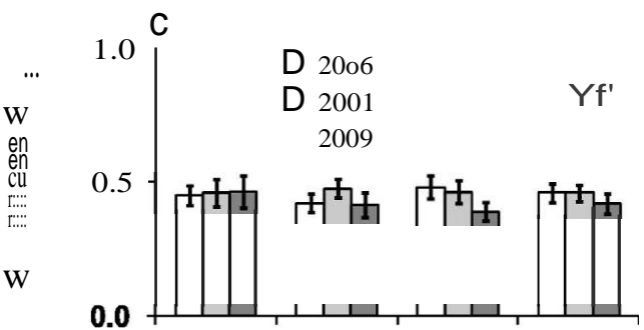
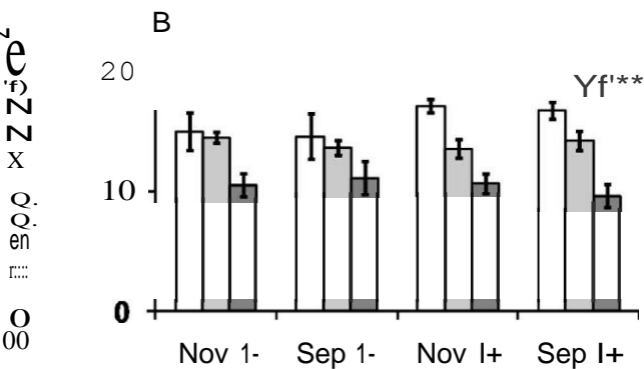
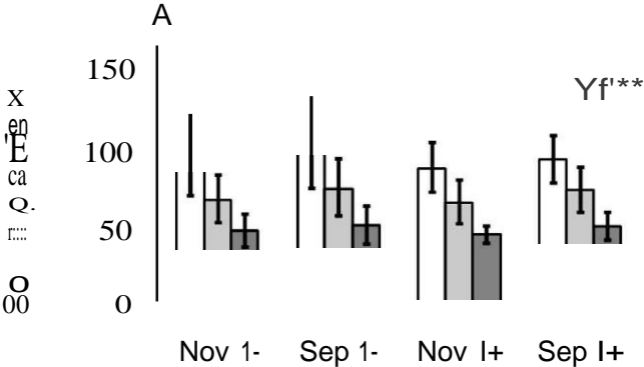
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Table 4. Matrix of Spearman coefficients r_s ($\times 100$) between numbers of *Primula* seedlings found in April 2009, numbers found in September 2009, *Primula* seedling survival (defined as the ratio between September and April numbers), and percentage cover values of bare ground, sown species, and unsown species (N = 16). Significant correlations (two-tailed test) in bold.

Seed _{APR}	Seed _{SEP}	Cover _{BG}	Cover _{SOWN}	Cover _{UNSOWN}	
6	70	15	-14	12	Survival
	67	-13	17	-12	Seed _{APR}
		-3	-8	16	Seed _{SEP}



Nov 1- Se 1- Nov I+ Se I+

