1 **The dynamics of designed plant communities of rosette forming forbs for use in supra-**

2 **urban drainage swales.**

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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 m^2. 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. supressed 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^{o}C, with a July mean temperature of

152 16.4^{o}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 / m^2 (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 m^2. *Primula rosea* 'Gigas' was sown at 150

179   seeds per m^2 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 m^2. 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

2.3 Data analysis

To avoid pseudo-replication, prior to statistical analyses, plant count data from the four

permanent quadrats per subplot, were summed, and biomass and cover data were averaged

across the four permanent quadrats).

With the exception of ordination analyses which were carried out using CANOCO,

version 4.5 (Ter Braak & Šmilauer, 2002), all statistical analyses were carried out using R,

version 2.12.2 (R Development Core Team, 2011).

To characterize sown community diversity, based on plant counts carried out in 2006,

2007 and 2009, we calculated species density and Smith-Wilson evenness (E_{var}) values

(Smith and Wilson, 1996) based on a reference area of $2.25m^2$ (i.e. the total area of the four

permanent quadrats in each subplot).   Prior to statistical analyses, counts of individuals and

of species were square-root transformed to improve distributional properties.

To analyse treatment and year effects on community diversity and on the numbers of

individuals of sown species individually and pooled together, we carried out repeated-

measures ANOVAs using R's 'car' package (Fox, 2011). In these analyses, experimental

plots represented subjects, irrigation represented a between-subjects factor, and year and

cutting date represented within-subjects factors. Greenhouse-Geisser correction was used to

adjust P-values associated with main and interaction effects of 'Year' for possible violations

of sphericity.

To analyse both general trends in community composition as well as cumulative

effects due to experimental treatments, we carried out two ordination analyses. As we were

interested in treatment effects on relative species composition, species count data was

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

3 Results

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

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

3.2 Changes in plant density between 2006 and 2009

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

299   poisonii, 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 × Year and Irrigation × 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 × 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 m^2, including *P.*

368 *rosea*, the species sown at 150 seed per m^2. *P. pulverulenta* had established an average of

369 about 20 plants per m^2 from a sown density of 100 seeds per m^2. 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 m^2 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 veri*s, 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

4.4 Management effects on the sown community

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

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

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

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

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

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

507 nectar value to native invertebrates, and the capacity of the *Primula* species to produce seed

508 and establish new seedling recruits. By 2009, November-cut plots were clearly more

509 floriferous than September-cut ones.

510 **4.5 The experimental plant community in relation to landscape architectural practice**

511 One of the most compelling lessons from this study is the importance of what happens

512 at the beginning of the establishment phase for the long-term performance of designed

513 vegetation. The 75mm deep sowing mulch facilitated high emergence and establishment of

514 the sown species whilst preventing the emergence of most weedy species from the underlying

515 soil. This provided the basis for dominance over the next 5 years by species that would not

516 normally be seen as competitive enough to do this. The experiment was set in mown wet

517 grassland in a public garden, surrounded by woodland, and weedy hedgerows-roadsides.

518 Competitive ruderals such as *Ranunculus repens, Agrostis stolonifera, Holcus lanatus*, as

519 well as tall species such as *Chamaenerion angustifolium*, and *Urtica dioica,* that often

520 colonise designed herbaceous planting from wind blown seed, were present close to the

521 experiment. The very low density of these colonists after five years appears to be due to three

522 factors; i) sowing mulches inhibited establishment in the first growing season, ii) the dense

523 overlapping canopies of the dominant *Primula* species eliminated many seedling colonists

524 that establishing after the first year through shading; iii) the site was very wet for much of

525 the year, reducing the pool of potential colonists to species adapted to anaerobic soils, such as

526 *Juncus* species.

527 Since this experiment was established in 2004, sowing mulches have been developed

528 by the lead author in commercial landscape practice to engineer a diversity of species-rich

529 herbaceous vegetation types, often on a large scale, throughout Britain (Richardson, 2011).

530 If complex, species-rich, vegetation is to be established on a large scale, for reasons of cost,

531 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 $F_{1,10}$	P	Irrigation (I) $F_{1,10}$	P	Cutting Date (C) $F_{1,10}$	P	C × I $F_{1,10}$	P	Year (Yr) $F_{2,20}$	$P_{\varepsilon 1}$	I × Yr $F_{2,20}$	$P_{\varepsilon 1}$	C × Yr $F_{2,20}$	$P_{\varepsilon 2}$	I × C × Yr $F_{2,20}$	$P_{\varepsilon 2}$	$\varepsilon_{1(GG)}$	$\varepsilon_{2(GG)}$
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
Primula alpicola	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
Primula beesiana	**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
Primula bulleyana	**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
Primula burmanica	**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
Primula chionantha	**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
Primula denticulata	**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
Primula japonica	**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
Primula poissonii	**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
Primula prolifera	**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
Primula pulverulenta	**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
Primula rosea '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
Primula secundiflora	**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
Primula sikkimensis	**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
Primula veris (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
Primula vulgaris (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
Cardamine pratensis (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
Dodecatheon jeffreyi	**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
Lychnis flos-cuculi (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
Persicaria milletii	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
Ranunculus acris (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
Succisa pratensis (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	0930	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

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

Analysis	Explanatory variables	Covariables	$\lambda 1$	$\Sigma \lambda_{CAN}$	$\Sigma \lambda$	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

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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		Primula mean weight		*Primula* standing biomass		Forb standing biomass		Graminoid standing biomass	
Source	**D.f.**	**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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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.

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

A

Yf'***

Nov 1-   Sep 1-   Nov I+   Sep I+

B

Yf'***

Nov 1-   Sep 1-   Nov I+   Sep I+

C

D 2006
D 2001
2009

Yf'

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

Car_prat

Pri_burm

Pri_pois   Ran_acri

Pri_alpi

Pri_slkk   Pri_bull

Lyc_flos   Pri_vulg

Year

Pri_prol   Per_mill

Pri_dent   Suc_prat

Pri_chio   Pri_begs

Pri_vert

Pri_secu

Pri_pulv

Pri_japo   Do _ief!

Pri_rosG

pMODEL < 0.001

-0.7   0.7

A — *Primula* spp.

400, 200, 0 (E × C, en ca E O m)

I*
C*

Nov 1-Nov I+ Sep 1-Sep I+

B — *Primula* spp.

6, 4, 2, 0

I*
C*

Nov 1-Nov I+ Sep 1-Sep I+

c — Otherforbs

400, 200, 0 (E × C, en ca E O m)

Nov 1-Nov I+ Sep 1-Sep I+

D — Graminoids

400, 200, 0 (E × C, en en C'G E O m)

Nov 1-Nov I+ Sep 1-Sep I+

	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Cardamine pratensis												
Dodecatheon jeffreyi												
Lychnis flos-cuculi												
Persicaria milletii												
Primula alpicola												
Primula beesiana												
Primula bulleyana												
Primula burmanica												
Primula chionantha												
Primula denticulata												
Primula japonica												
Primula poissonii												
Primula prolifera												
Primula pulverulenta												
Primula rosea 'Gigas'												
Primula secundiflora												
Primula sikkimensis												
Primula veris												
Primula vulgaris												
Ranunculus acris												
Succisa pratensis												

in leaf
in flower