

1 **Resilience to extreme flooding shown by both hydric and mesic wetland plant species**

2

3 Sarah J. Brotherton, Chris B. Joyce, Maureen J. Berg and Graeme J. Awcock

4

5 Centre for Aquatic Environments, School of Environment and Technology, University of

6 Brighton, Brighton, United Kingdom.

7

8 Correspondence: C.B. Joyce, Centre for Aquatic Environments, School of Environment and

9 Technology, University of Brighton, Cockcroft Building, Lewes Road, Brighton, BN2 4GJ,

10 United Kingdom. Email: C.B.Joyce@brighton.ac.uk

11

12 Short title: Resilience to extreme flooding by wetland plants

13

14

15

16

17

18

19

20

21

22

23

24

25

26 **Abstract**

27 Global climate change models forecast an increasing frequency and duration of extreme flood
28 events, including during the growing season. In this mesocosm experiment, the survival,
29 growth and flowering of two hydric and two mesic wetland plant species were monitored
30 under two extreme flood regimes, namely repeated 2- and 7-day floods, and compared to
31 unflooded conditions. Plant survival was not significantly affected by flooding but species
32 showed different growth and flowering responses to the flood regimes. The hydric species
33 *Cardamine pratensis* showed contrasting responses to floods with significantly more
34 flowering stems and longer leaves in the 2-day regime, but delayed and poorer flowering in
35 the 7-day regime. *Juncus articulatus*, the other hydric species, responded most actively to 7-
36 day flooding, with significantly longer leaves, taller and more abundant flowering stems, and
37 more flowers than in unflooded conditions. The mesic species *Ranunculus acris* showed
38 variable growth and phenological responses to flooding while *Scorzoneroideis autumnalis* was
39 most affected by the 7-day flood regime, producing significantly shorter leaves and flowering
40 stems, and fewer flowers earlier in the season, compared to unflooded conditions. Overall,
41 repeated 7-day floods had a greater impact on plant performance than 2-day flood events. All
42 four species showed resilience to extreme flooding, irrespective of whether they were classed
43 as hydric or mesic, but there was differential tolerance between species. This suggests that
44 wetlands should be able to sustain vegetation under flooding extremes induced by climate
45 change but community composition, biodiversity, and wetland services will all be affected.

46

47 **Keywords:** Climate change, flowering, functional traits, hydrology, mesocosm

48

49 **1 Introduction**

50 Global climate change models forecast an increasing frequency, intensity and duration of
51 extreme climate events (IPCC, 2007), such as droughts and flooding, the latter often induced
52 by storms and intense rainfall. The timing of flooding is also shifting, with unseasonal and
53 delayed winter floods in some regions (Blöschl et al., 2017) potentially extending flooding into
54 the growing season. In recent years, unseasonal storms have caused widespread and
55 devastating summer floods in Europe (Kundzewicz, Pińskwar, & Brakenridge, 2013) while in
56 the USA stream gauge records provide strong evidence for an increasing frequency of floods
57 (Mallakpour & Villarini, 2015). Flooding significantly alters ecosystem functioning, including
58 plant production and communities (Kreyling, Wenigmann, Beierkuhnlein, & Jentsch, 2008;
59 Arnone et al., 2011), affecting ecosystem services that benefit the global population.
60 Consequently, extreme climate events may be more important ecologically than incremental
61 climate trends (Tebaldi, Hayhoe, Arblaster, & Meehl, 2006; Jentsch, Kreyling, &
62 Beierkuhnlein, 2007; Smith, 2011; Reyer et al., 2013; Thompson, Beardall, Beringer, Grace,
63 & Sardina, 2013). The need for greater understanding of the ecological impacts of extreme
64 climate events is, therefore, pressing (Jentsch, Kreyling, & Beierkuhnlein, 2007; Smith, 2011;
65 Reyer et al., 2013; Niu et al., 2014), especially as society seeks to adapt to, and mitigate, climate
66 change and its effects.

67

68 The specific impacts of extreme climate events on wetlands are not known, despite the vital
69 ecosystem services they provide, which include flood attenuation, sediment and carbon storage,
70 protection from erosion, removal of pollutants, and agricultural production (Joyce, Simpson,
71 & Casanova, 2016). Although some wetlands are characterised by considerable hydrological
72 variability, such as prairie potholes that experience drought and deluge (Winter & Rosenberg,
73 1998; van der Kamp, Hayashi, Bedard-Haughn, & Pennock, 2016), research into the impacts

74 of extreme climate events on the natural environment is still in its infancy, with data collected
75 mainly from dry or mesic grasslands (e.g. Fay, Carlisle, Knapp, Blair, & Collins, 2003; Sherry
76 et al., 2007; Kreyling, Wenigmann, Beierkuhnlein, & Jentsch, 2008; Jentsch et al., 2011).
77 There is a growing appreciation that repeated extreme climate events may be more important
78 than single events and that investigations should therefore include environmental responses to
79 multiple events (Bailey & van de Pol, 2016). Field observations indicate that intense or
80 prolonged flooding significantly and rapidly affect plant distribution and community
81 composition (Vervuren, Blom, & de Kroon, 2003; Toogood & Joyce, 2009), suggesting that
82 the magnitude and duration of extreme events will be critical for wetlands. Moreover, extreme
83 events may have particularly important consequences for wetland stakeholders, as they can
84 prevent or delay vital management activities such as harvesting or livestock grazing, leading
85 to loss of income or nature conservation benefits (Joyce, Simpson, & Casanova, 2016).

86

87 Wetland plants are likely to be significantly affected by more frequent flooding, particularly if
88 events are of longer duration, and unseasonal, even though many plants are adapted to
89 inundation. Casanova and Brock (2000) suggest that flood duration may be a more important
90 factor than either depth or frequency for wetland plant community composition. Changes of
91 only 10% in flood duration may be enough to eliminate some wet grassland species from
92 floodplains (Campbell, Keddy, Broussard, & McFalls-Smith, 2016). Flooding during the
93 summer growing season in temperate regions has a more immediate impact on plant survival
94 than in winter, when plants have slow metabolic rates with little growth (van Eck, van de Steeg,
95 Blom, & de Kroon, 2004; van Eck, Lenssen, van de Steeg, Blom, & de Kroon, 2006). Indeed,
96 Johansson and Nilsson (2002) reported summer flood duration to be the most important factor
97 affecting survival and growth of a range of Boreal riparian plant species. Flowering is a
98 particularly sensitive indicator of changes in environmental conditions such as flooding (Blom

99 et al., 1990), air temperature (Hovenden, Wills, Vander Schoor, Williams, & Newton, 2008)
100 and drought (Jentsch, Kreyling, Boettcher-Treschkow, & Beierkuhnlein, 2009). A relationship
101 between accelerated flowering and climate warming has been well established, for example in
102 Great Britain (Fitter & Fitter, 2002), but research on relationships between flooding and
103 flowering in different plant species is lacking.

104

105 The ability for wetland plants to be resilient in flooded environments is related to their
106 ecological adaptations and functional traits, which can therefore be used to elucidate the
107 impacts of climate change. Resilience incorporates the flexibility to recover from a disturbance
108 and return to a previous functioning state (Mori, 2011) so that a species or community persists
109 through time and space (Grimm & Wissel, 1997). There are two main adaptive strategies plants
110 employ to survive flooding disturbance, namely ‘quiescence’ or ‘escape’ (Bailey-Serres &
111 Voesenek, 2008). With quiescence, a plant may slow its metabolic rate and other functions to
112 sustain life while fully submerged (Bailey-Serres & Voesenek, 2010), and it is therefore more
113 common in amphibious species. Many wetland species are more likely to use an escape
114 strategy, whereby a plant can elongate leaves or stems rapidly (Banach et al., 2009) so that
115 these are maintained above water. Generally, this adaptation is found in species typical of
116 wetland environments that are frequently submerged (e.g. riparian habitats), and is less
117 common in species from habitats such as grasslands that only experience saturated soil (Banach
118 et al., 2009). Interactions between plants can mediate the effects of functional adaptations to
119 water levels within plant communities (Brotherton & Joyce, 2015), and hydrological niches
120 have been shown to be sensitive controls on plant co-existence and distribution in wetland
121 communities (Silvertown, Dodd, Gowing, & Mountford, 1999).

122

123 It is evident that extreme flooding due to climate change will likely have profound effects on
124 plant performance. However, the impacts of increasing frequency and duration of unseasonal
125 flooding, as predicted in climate change scenarios, has not been investigated for wetland
126 species. This mesocosm experiment examined species typically found in saturated and often
127 inundated soils, termed hydric species, and mesic species of moist soils with little if any
128 waterlogging, to elucidate the impacts of extreme flooding regimes on the performance of
129 wetland plants. Extreme flooding was represented by flood events of two durations repeated
130 through the growing season. Repeated flood treatments are uncommon in wetland mesocosm
131 experiments where flooding is often continuous for the duration of the experiment (e.g. Loeb,
132 Lamers, & Roelofs, 2008; Luo, Xiw, Chen, & Li, 2010; Cusell, Lamers, van Wirdum, &
133 Kooijman, 2013) or conducted only once (e.g. van Eck, van de Steeg, Blom, & de Kroon, 2004;
134 Yetisir, Çaliskan, Soylu, & Sakar, 2006; Nielsen, Podnar, Watts, & Wilson, 2013). Plant
135 performance was assessed using survival, growth and flowering. It was hypothesized that the
136 hydric species would be more resilient and show better performance than mesic species in
137 flooding conditions, especially in the more severe flood regime. Experiments combining plant
138 traits and extreme climate events are rare (Jentsch et al., 2011), and even controlled
139 experiments have tended to use conservative climate treatments, but the mesocosm approach
140 used in this study enabled the impacts of intense but realistic flooding regimes to be monitored
141 in detail using a suite of metrics applied to individual plants.

142

143 **2 Methods**

144 2.1 Flood treatments

145 Experimental flood treatments were motivated by global predictions of more frequent,
146 extended flood events, which may be repeated through the growing season. More specifically,

147 to mimic realistic scenarios and avoid underestimation, flood durations and frequency were
148 based upon those observed for the River Arun in south eastern England during the extremely
149 wet summer of 2012, which was the wettest on record in England, and second wettest in Britain
150 (www.metoffice.co.uk, 2014). In 2012, river level data from monitoring stations along the
151 Arun showed that the river breached its banks eight times between March and September,
152 inundating the floodplain wetlands at Amberley (50° 55' 02.9" N, 0° 32' 12.3" W), most
153 frequently for two days but for up to seven days. Thus, experimental treatments consisted of
154 repeated flood events lasting for two days (48 hours) and seven days (168 hours), as well as
155 unflooded mesocosms that represented control conditions. Eight flood events of the two
156 different durations were applied between the end of March and the beginning of September
157 2014, initiated every 21 days so that all flood treatments commenced at the same time.

158

159 2.2 Plant species

160 Four plant species were selected to characterise either hydric or mesic wetland communities
161 and environments (Table 1). All four species have mostly similar traits except for their
162 hydrological preferences (Table 1). They show closely comparable light requirements and
163 nutrient preferences (Hill, Preston, & Roy, 2004), and all are perennials with similar life history
164 strategies (Grime, Hogson, & Hunt, 1992). Ellenberg values for moisture indicate that the
165 hydric species *Cardamine pratensis* and *Juncus articulatus* both show a preference for
166 saturated soils (Hill, Preston, & Roy, 2004), and they can withstand extended waterlogging
167 (Gowing et al., 2002), while the mesic species *Ranunculus acris* and *Scorzoneroides*
168 *autumnalis* prefer moist environments and are tolerant of dry soil conditions (Gowing et al.,
169 2002).

170

171 The plant species are common components of the English flora and valuable indicators of
172 hydrological regimes across their international distributions (Table 1). At the Amberley
173 floodplain site, which provided the template for the experimental flood scenarios, the two
174 hydric species were found in semi-permanently saturated, frequently inundated grasslands
175 while the two mesic species were restricted to seasonally wet grasslands that rarely flood. The
176 hydric species *C. pratensis* is found across a range of habitats in the northern hemisphere (Table
177 1) including wet woodland, wet and moist grasslands, and riparian areas (Rodwell, 1991;
178 Rodwell, 1992). *J. articulatus* is a hydric species native to many wetland habitats across much
179 of the northern hemisphere and was introduced in the southern hemisphere (Table 1), where it
180 is considered invasive (Smith & Brock, 1996). It is tolerant of shallow standing water and
181 fluctuating water levels (Smith & Brock, 1996). *R. acris* is a widely distributed mesic species
182 native to much of Europe and Asia that has been introduced to other continents (Table 1). It is
183 common in a range of habitats with damp soils from unimproved meadows to agricultural and
184 amenity grasslands (e.g. lawns, parks) (Rodwell, 1992). *S. autumnalis* is widespread in Eurasia
185 and introduced into North America (Table 1). It is common to amenity, agricultural and other
186 grassland and open habitats (Hill, Mountford, Roy, & Bunce, 1999), although this mesic
187 species is also associated with wetter grassland communities (Rodwell, 1992).

188

189 2.3 Mesocosm and experimental design

190 Mesocosms were established outside on a level, unshaded site of approximately 50 m² at the
191 University of Brighton Moulsecoomb campus, Brighton, UK, (50° 50' 40.4" N, 0° 07' 06.6"
192 W). There were 36 units, each comprising a 15 l plastic pot placed inside a 40 l plastic bucket
193 with a tap inserted 5 cm above the bucket base for controlling water levels. The tap drained
194 excess water during and after precipitation and following flooding treatment. All pots were

195 lined with root exclusion fabric to prevent roots from escaping through drainage holes. The
196 fabric was covered with a layer of pea gravel to aid drainage. The pots were filled to within 5
197 cm of the top with a 2:1:1 (by volume) potting mixture of commercially available washed sharp
198 sand, topsoil with screened and sterilised loam, and commercial compost (Araya, Gowing, &
199 Dise, 2010).

200

201 Seedlings of the four experimental species were sourced from a commercial supplier (British
202 Wild Flower Plants, Norfolk, UK), ensuring that each seedling of each species was of similar
203 physiognomy (e.g. with four leaves). Prior to planting, the mesocosm pots were watered and
204 a mixture of compost and vermiculture was incorporated into the surface layer of the potting
205 mixture to aid establishment of the plants. The seedlings were planted and immediately watered
206 in September 2013, then allowed to establish over winter for treatments to commence in March
207 2014. No further additions to the growing medium were made and plants did not require any
208 further watering after September. All plants survived over winter except for three *C. pratensis*
209 individuals, which were replaced in mid-January 2014. Pots were placed randomly into mixed
210 rows to eliminate location bias for any treatment, with the pots remaining in these positions
211 throughout the experiment.

212

213 The water in all mesocosms was maintained at a base level 5 cm above the bottom of the
214 buckets, which was approximately 16 cm below the growing medium surface, except when
215 flooding treatments were applied. To place mesocosms into flooded conditions, the taps on the
216 buckets were closed and water was applied into the top of the buckets using a hose connected
217 to a mains supply. Tap water was used for convenience, in common with many other
218 mesocosm studies (e.g. Weiher & Keddy, 1995; van Eck, van de Steeg, Blom, & de Kroon,

219 2004; Yetisir, Çaliskan, Soylu, & Sakar, 2006; Nygaard & Ejrnæs, 2009). Water was directed
220 into the buckets rather than the pots to minimise disturbance to the growing medium. Flood
221 water levels were maintained at the rim of the buckets, approximately 7 cm above the growing
222 medium surface. Consequently, plants were submerged by initial flood treatments but
223 subsequently grew above water levels. During flood treatments, buckets were inspected every
224 two days and water levels were replenished if they had fallen due to evapotranspiration. Outside
225 of flooding treatments, the water levels were monitored weekly in the spring but more
226 frequently through the summer and augmented to the base level when necessary.

227

228 2.4 Plant metrics and monitoring

229 Each mesocosm pot contained six plants of either the two hydric or the two mesic species, with
230 three individuals per species. There were six replicate pots per species combination, giving 18
231 plants per species per treatment. All plants were monitored for survival, growth and flowering
232 in weekly surveys from 17-Mar-2014 until 8-Sep-2014 inclusive. *J. articulatus* plants were
233 trimmed to 5cm so that all plants began the experiment at the same height; this was not feasible
234 for the other species due to their morphology. However, statistical analysis showed that there
235 were no significant differences in plant metrics between treatments in March 2014, prior to the
236 treatments being applied. Plants were individually tagged before the experiment using
237 coloured plastic ties, which ensured that metrics for each plant were monitored consistently.

238

239 Plant survival monitoring comprised a visual assessment of whether each plant was alive at the
240 time of survey, with no evaluation of its condition or likelihood of survival to the next survey.
241 Plant growth was recorded at each survey by i) measuring maximum basal leaf length, ii)
242 counting the number of flowering stems, and iii) measuring maximum flowering stem height

243 including the flowering head. Flowering stems were measured from the node with the main
244 stem for *R. acris*, and from emergence from basal leaves for *C. pratensis* and *S. autumnalis*.
245 Flowers appear on the leaf stems on *J. articulatus*, so for this species the total height including
246 flowering head was recorded. Flowering assessment at each survey incorporated i) a count of
247 the number of fully open flowers on each plant, except for *J. articulatus* where the number of
248 flowering stems was counted (as above) because individual flowers were too small and
249 numerous to count accurately, and ii) an evaluation of phenology. Flowering phenology was
250 recorded using a categorical classification based on the reproductive stage of the most advanced
251 flower on each plant, following Price and Waser (1998) and Sherry et al. (2007): S1 - Unopened
252 buds; S2 - Open flowers; S3 - Old flowers defined as postanthesis; S4 - Petals gone and initial
253 fruit; S5 - Expanded fruit; and S6 - Dehisced fruit.

254

255 2.5 Data analysis

256 Unweighted means were used so that all individual plants contributed equally to total values.
257 It is not uncommon in ecological studies for multiple plants to be grown and analysed from the
258 same mesocosm without nesting the replicate growing spaces (e.g. Kercher & Zedler, 2004;
259 Kreyling, Wenigmann, Beierkuhnlein, & Jentsch, 2008; Nygaard & Ejrnæs, 2009).
260 Furthermore, to test for statistical dependency, all individuals were Z-scored per metric, and
261 there were no instances of multiple individuals from any one mesocosm showing an outlying
262 trend in any metric.

263

264 Continuous data sets were examined for normal distribution with the Anderson-Darling test,
265 and the Levene's test for homogeneity of variance. Exceptionally, outlier data for individual
266 plants were removed before tests were performed where their presence profoundly skewed the

267 distribution of data (Osborne & Overbay, 2004), as indicated in the relevant results. To account
268 for unrepresentative individual plants, the phenological classification was complemented by
269 the identification of the day by which proportions of the plants for each species were in open
270 flower (S2).

271

272 Generalized Linear Models, based upon a Poisson loglinear model type, were used with
273 Bonferroni corrections to assess whether there were any significant differences between
274 treatments for the number of stems and number of flowers. Post-hoc examinations used Least
275 Significant Difference (LSD). A one-way ANOVA was used for measures of stem height with
276 Tukey post-hoc tests. Linear Mixed-Effects Modelling was utilised with Bonferroni correction
277 for analysing repeated measures of leaf length, with LSD post-hoc testing, for dates at the
278 beginning, middle and end of the experiment. The test used the heterogeneous Toeplitz
279 repeated covariance type and Restricted Maximum Likelihood estimation. Significant
280 differences for all data analysis are reported where $P < 0.05$ or their Bonferroni equivalents.

281

282 **3 Results**

283 3.1 Survival

284 There were no significant differences in plant survival between any of the flooding treatments
285 for any of the four species. At the end of the experiment in September, all *J. articulatus* and
286 *R. acris* plants survived in all three treatments. One *C. pratensis* plant died (from 7-Jul) in the
287 unflooded control conditions and two plants of *S. autumnalis* died, one each in the control
288 (from 18-Aug) and 7-day flood treatments (on 8-Sep). Both *S. autumnalis* plants had flowered
289 and produced seeds before dying, and were therefore included in other analysis where
290 appropriate.

291

292 3.2 Growth

293 *Leaf length*

294 Leaf length for all species was compared at the beginning (17-Mar), middle (9-Jun) and end
295 (8-Sep) of the experiment. The results of Linear Mixed-Effects Modelling of treatment, time
296 and an interaction of these two factors suggest that time was a highly significant factor for all
297 species ($P < 0.001$; Table S-1). Leaves generally extended over time in nearly all treatments,
298 except for *S. autumnalis* where leaves were longest during rather than at the end of the
299 experiment (Figure 1). All species also showed significant interactions between time and flood
300 treatment ($P \leq 0.003$; Table S-1).

301

302 Leaf lengths at the beginning of the experiment were not significantly different between
303 treatments for any of the species (Figure 1). Longer leaves were produced by *C. pratensis*
304 plants in the flooded treatments compared to the controls, with significantly longer leaves
305 during the experiment in the 7-day flooding and by the end of the experiment in the 2-day
306 floods (Figure 1). *J. articulatus* produced significantly longer leaves in the 7-day flooding than
307 both other treatments at the mid and end dates, while plants treated to 2-day flooding had
308 significantly shorter leaves at the end than plants in control or 7-day flood conditions (Figure
309 1). Leaf lengths for *R. acris* were variable over time but this species produced significantly
310 longer leaves in the 7-day flood scenario than either of the other treatments (Figure 1). Both
311 flooding treatments resulted in significantly longer leaves compared to the control for *S.*
312 *autumnalis* at the mid-period of the experiment, but then leaf length rapidly decreased in the
313 7-day flooding and was significantly smaller than the other two treatments by the end (Figure
314 1).

315

316 *Flowering stem abundance*

317 All individual plants produced flowering stems in all treatments for all species except for *C.*
318 *pratensis*, for which eight plants from 18 produced flowering stems in the unflooded control
319 conditions compared to 15 in the 2-day and 14 in the 7-day flood treatments. There were
320 significant differences in the abundance of flowering stems between flooding treatments for
321 two species (*C. pratensis* $P = 0.013$, *J. articulatus* $P = 0.001$; Table S-2). The mean number
322 of flowering stems produced per flowering *J. articulatus* plant was significantly greater in the
323 7-day flood treatment compared to the 2-day flood treatment or control (Figure 2). *C. pratensis*
324 produced significantly more stems in the 2-day than the 7-day flood treatment, with the control
325 plants intermediate (Figure 2). There was no significant difference between the treatments for
326 *R. acris* nor *S. autumnalis* (Figure 2; Table S-2).

327

328 *Flowering stem height*

329 There was a significant difference in flowering stem height for *J. articulatus* ($P = 0.001$) and
330 *S. autumnalis* ($P = 0.006$) between treatments (Table S-3). Plants treated to 7-day floods had
331 significantly taller flowering stems for *J. articulatus*, and significantly smaller for *S.*
332 *autumnalis*, than plants in the other two treatments (Figure 3). There was no significant
333 difference in the flowering stem height between treatments for both *C. pratensis* and *R. acris*
334 (Table S-3).

335

336 3.3 Flowering

337 *Flower abundance*

338 The mean number of flowers produced per flowering plant was significantly different between
339 treatments for *J. articulatus* ($P = 0.001$) and *S. autumnalis* ($P < 0.001$) but not for *C. pratensis*
340 nor *R. acris* (Table S-4). *J. articulatus* produced significantly more flowers in the 7-day flood
341 scenario than the other two treatments, which were not significantly different from each other
342 (Figure 4). In contrast, there were significantly fewer flowers produced by *S. autumnalis* under
343 repeated 7-day flooding compared to the other two treatments, which were not significantly
344 different from each other (Figure 4). Thus, both significant differences in flowering abundance
345 shown by the four species involved the 7-day flood treatment.

346

347 *Flowering phenology*

348 The earliest *C. pratensis* plant flowered (S2 and S3) two weeks earlier in the 2-day flood
349 treatment than the two other treatments but there was little difference in the timing of fruiting
350 (S5 and S6) later in the season (Figure 5). In contrast, data indicated that increasing flood
351 duration progressively delayed flowering in this species, with at least 50% of unflooded
352 plants in flower after 105 days of the year, after 113 days for 2-day flooding, and after 133
353 days for floods lasting 7 days (Figure 6). Flowers on *J. articulatus* started to open (S2) seven
354 days earlier when subjected to 2-day or 7-day flood scenarios compared to unflooded control
355 conditions but subsequently there was no difference in phenological development of this
356 species between treatments (Figure 5), with at least 50% of plants flowering in all treatments
357 at 182 days (Figure 6). For *R. acris*, flowering was earlier in the 2-day flood treatment than
358 the other two treatments until fruit had formed (S5) while in the 7-day flood treatment buds

359 formed (S1) at a similar time to the control plants but most other stages were delayed by up to
360 two weeks (Figure 5). Indeed, it was 140 days into the year before 50% of *R. acris* plants that
361 had been repeatedly flooded for 7-days were flowering, which was seven days later than both
362 the control and 2-day flooded plants (Figure 6). *S. autumnalis* plants in both flooding
363 treatments began budding (S1) seven days earlier, and were shedding seeds (S6) 14 days
364 earlier, than control plants (Figure 5). Furthermore, 50% of *S. autumnalis* plants subjected to
365 any flooding were flowering after 203 days of the year, seven days earlier than unflooded
366 plants in control conditions (Figure 6).

367

368 **4 Discussion**

369 4.1 Species responses to extreme flooding

370 All four wetland plant species in this mesocosm experiment showed some resilience to extreme
371 flooding represented by 2- or 7-day events repeated through the growing season. Overall, there
372 were more significant plant responses to 7- than 2-day flooding, compared to unflooded
373 conditions, indicating that more severe flooding had a greater impact on performance.
374 However, survival was largely unaffected, irrespective of whether species were classed as
375 hydric or mesic functional types, as only three of the 216 individual plants monitored in this
376 study died. Thus, the extreme but realistic flood intensities implemented here, based upon
377 exceptional field conditions, were insufficient to cause plant deaths. Other studies have also
378 indicated the resilience of the experimental species to flooding. For example, He et al. (1999)
379 and Banach et al. (2009) suggest that survival in *R. acris* is possible after six weeks of flooding
380 while Johansson and Nilsson (2002) suggest *S. autumnalis* can survive inundation for up to
381 200 days. However, this study differed in testing frequently repeated flood events rather than
382 a single inundation or low frequency flooding, and other studies have shown that small
383 hydrological changes can induce major plant effects, including loss of species (Toogood, Joyce,

384 & Waite, 2008; Campbell, Keddy, Broussard, & McFalls-Smith, 2016). Moreover, the flood
385 regimes examined in this study initiated significant sub-lethal effects. Nevertheless, this study
386 indicates that floodplain wetland plants may survive future climate-driven flooding extremes,
387 at least in the short-term.

388

389 In this experiment, species with hydric characteristics did not generally perform more
390 effectively than mesic species when flooded, where enhanced performance was indicated by
391 larger plants with more flowers. This implies that scientists and practitioners need not limit
392 themselves to hydric plants when designing or creating wetlands where extreme flooding
393 scenarios are forecast, and that a range of species may be suitable. Furthermore, neither hydric
394 nor mesic species responded consistently to flooding. Instead, differential responses at the
395 species level were evident, despite the species having similar functional traits other than
396 hydrological optima.

397

398 The hydric species *C. pratensis* showed contrasting responses to the flood conditions. Only
399 eight plants flowered in unflooded conditions, almost half the number observed in the two flood
400 regimes, suggesting that flooding had a positive effect on flowering. The species produced
401 significantly more flowering stems, more flowers and longer leaves in the 2-day flooding
402 regime. The 7-day flooding was detrimental to its flowering performance, however, with
403 significantly fewer stems and reduced abundance of flowers (by 30% compared to plants that
404 flowered in unflooded conditions), and flowering was delayed by up to four weeks. There is
405 no comparable published research examining the effects of flooding on *C. pratensis* but it
406 seems that this species can tolerate or benefit from short duration flooding but may be impaired

407 by extended flooding, which would be detrimental to many insect species as its flowers provide
408 food in early Spring (Grime, Hodgson, & Hunt, 1992).

409

410 Of all the species tested, the hydric species *J. articulatus* responded most actively to extreme
411 flooding, specifically repeated 7-day floods. The species showed significant leaf elongation,
412 significantly taller flowering stems, and significantly enhanced flower abundance (by 27%) in
413 the longer flooding treatment, compared to unflooded conditions. Plants also began flowering
414 one week earlier when flooded. The graminoid form of *J. articulatus* may have been beneficial
415 in this flooding experiment. Wright et al. (2017) observed that graminoids were less affected
416 by extreme flooding than herbaceous forbs and Campbell, Keddy, Broussard, and McFalls-
417 Smith (2016) noted a shift from broadleaved to graminoid wetland species as flood duration
418 increased. Graminoids can adopt a more erect form and develop a taller canopy than forbs to
419 sustain aerial gas exchange in flooded grasslands (Striker, Mollard, Grimoldi, León, & Inausti,
420 2011), and the generation of aerenchyma induced by flooding was found to weaken roots in
421 forbs but not graminoids (Striker, Inausti, Grimoldi, & Vega, 2007). The repeated flooding
422 applied in this experiment may also have suited *J. articulatus*. Smith and Brock (1996) found
423 that the growth of this species was greatest in fluctuating water levels, and performance was
424 poorest in saturated soil conditions. The species can prevent others establishing in wetlands
425 when it becomes dominant, including those of high conservation value (McKendrick, 1995).

426

427 The mesic species *R. acris* showed variable results in response to flooding but no significant
428 differences between flood regimes except for leaf growth, indicating resilience to flooding. *R.*
429 *acris* produced significantly longer leaves in repeated floods of both 2- and 7-day duration. It
430 began flowering earlier under 2-day floods than in unflooded conditions but under 7-day

431 flooding flowering was generally delayed by a week, and seed shedding by two weeks. Banach
432 et al. (2009) also suggest that this species is somewhat tolerant of inundation, as it was one of
433 just two species from permanently saturated wet grassland in their study to withstand infrequent
434 submersion for a period of up to six weeks, albeit with with a mortality rate of 20-30%.

435

436 *S. autumnalis* was the species most significantly and negatively affected by the more extreme,
437 7-day flooding regime, although its performance in the less severe, 2-day flooding was similar
438 to unflooded conditions. This mesic species produced significantly shorter leaves and
439 flowering stems in the 7-day flooding compared to unflooded conditions. Longer flood events
440 significantly reduced flower abundance (by 75%). Flowering phenology for *S. autumnalis*
441 generally advanced by between one and three weeks in flooded compared to unflooded
442 conditions. Results therefore suggest a restricted tolerance to flooding for this species, which
443 limits its distribution in wetland habitats. *S. autumnalis* may have a sensitive flood duration
444 threshold, such that it is able to tolerate short duration flooding but may not possess the
445 adaptations necessary to withstand extended flood events. For example, Johansson and Nilsson
446 (2002) observed that although *S. autumnalis* survived flooding for long durations along a range
447 of rivers, it showed no growth. The species is therefore likely to decrease under future climate
448 change scenarios with more extreme flooding regimes (IPCC, 2007).

449

450 4.2 Plant adaptations and resilience

451 All species in this study showed resilience to flooding through significant elongation of leaves
452 and/or flowering stems, a response to ensure that they are above the water level (Pierik, van
453 Aken, & Voeselek, 2009). In this experiment, leaves generally showed more elongation than

454 stems. Indeed, all species showed significant leaf elongation during the experiment in the most
455 extreme flooding regime of repeated 7-day floods, although this growth was not always
456 sustained until the end of the season (Figure 1). Garssen, Baattrup-Pedersen, Voesenek,
457 Verhoeven, and Soons (2015) suggest stem elongation to be the most important factor in
458 avoiding flooding. In this experiment however, significant stem elongation was only evident
459 in the hydric species *J. articulatus* subjected to 7-day floods.

460

461 There is a paucity of studies examining flower abundance and extreme climate events but this
462 experiment suggests that flowering responses to flooding are species-specific and related to the
463 duration of inundation. Plants repeatedly flooded for two days tended to produce more
464 flowering stems and flowers than unflooded plants, but not significantly so. The hydric species
465 *J. articulatus* supported significantly more flowering stems when flooded for seven days.
466 However, mesic *S. autumnalis* plants flooded for seven days produced significantly fewer
467 flowers than unflooded plants or those inundated for two days. Flooding may influence
468 flowering abundance variably by moderating temperature, creating disturbance or inducing
469 stress. For example, a decline in floret density was observed in *Juncus gerardii* as tidal
470 inundation increased (Watson, Wigand, Cencer, & Blount, 2015) while flooding stimulated
471 shoot elongation with enhanced seed production in the floodplain species *Rumex maritimus*
472 (van der Sman, Voesenek, Blom, Harren, & Reuss, 1991). Predictions for an increasing
473 incidence, magnitude and duration of flooding (IPCC, 2007) suggest that flowering responses
474 will become more variable and contrasting between species in the future.

475

476 This study shows that the extreme flooding regimes predicted under climate change scenarios
477 can substantially influence flowering phenology. While increased air temperatures due to long-

478 term climate warming are known to advance flowering (Fitter & Fitter, 2002), there is a lack
479 of research investigating phenological changes due to flooding, even though it may act as an
480 environmental cue. Wetland plants can remain quiescent to persist during flooding, or can
481 accelerate reproduction in response to flood disturbance by flowering and seeding earlier (see
482 Blom et al., 1990). In this experiment, species tended to show the latter behaviour. The hydric
483 species *J. articulatus* first flowered a week earlier when flooded and the flowering phenology
484 of the mesic species *S. autumnalis* advanced by at least a week in flooded conditions. These
485 plants may be responding to increased water availability, which might not be guaranteed later
486 in the growing season, or initiating rapid flowering and seed set in case of continued,
487 detrimental flooding. However, flowering by the hydric species *C. pratensis* was on average
488 delayed by up to four weeks when flooded repeatedly, even though the first flower in the 2-day
489 floods opened two weeks earlier than unflooded plants. Some variation in phenology of
490 individual plants is not uncommon, and is associated with phenotypic plasticity (Toräng,
491 Ehrlén, & Ågren, 2010). Shifts in phenology induced by flooding could not only affect plant
492 survival in the longer-term but will impact the invertebrates that feed on their flowers and
493 seeds.

494

495 While all species showed some resilience and survived extreme flooding, irrespective of
496 whether they were classed as hydric or mesic, care should be taken when extrapolating these
497 results from mesocosm experiments to wetland field environments. Species differed in their
498 functional responses, indicating that adaptations to extreme flooding would confer competitive
499 advantages for some species over others in plant communities. Indeed, competition may limit
500 the distribution of species in wetland communities to particular hydroperiods. For example,
501 He et al. (1999) suggest *R. acris* is more tolerant of inundation than its range within river
502 floodplains would indicate and indeed this mesic species performed better than expected in

503 extreme flood regimes in this study given its preference for non-saturated soils (Gowing et al.,
504 2002). In contrast, models from Gowing et al. (2002) suggest that *S. autumnalis* should be
505 better adapted to the extended flooding applied in this study than the results indicate. Plants of
506 this species were grown in mesocosms with *R. acris*, which performed relatively well in severe
507 floods compared to *S. autumnalis*, and it is possible that the two species interacted.
508 Experimental results for the two hydric species *C. pratensis* and *J. articulatus* indicated
509 adaptations to either shorter-term or longer-term flooding respectively, suggesting that the
510 specific nature of future flooding will determine species distribution and community
511 composition.

512

513 **5 Conclusions**

514 The results of this study suggest that wetlands can sustain a diversity of vegetation under
515 flooding extremes due to functional resilience, but that the variable responses of species to
516 flood duration and repeated unseasonal flooding will affect community composition and
517 wetland services. Flooding induced phenological shifts, which are likely to disrupt pollinator
518 interactions (Memmott, Craze, Waser, & Price, 2007) and plant reproduction. For example,
519 flowering by *S. autumnalis*, which provides an important food resource for a diversity of insects
520 late in the season in temperate mesic habitats, was advanced and reduced in the most severe
521 flood regime. In contrast, *J. articulatus* produced significantly more flowers in the most
522 extreme flood scenario, which may benefit waterfowl that feed on this species. Rare and
523 threatened wading birds may be affected by plant community changes generated by flooding
524 extremes as vegetation structure plays a key role in nest site selection (Durant, Tichit, Fritz, &
525 Kernéis, 2008). The livelihoods of millions of people globally depend upon harvesting wetland
526 biomass, such as for fodder (Joyce, Simpson, & Casanova, 2016). Differential species

527 responses to extreme flooding will lead to changes in forage quality, and people may need to
528 adapt management activities such as cutting and grazing to accommodate phenological
529 changes. This research has indicated that wetland stakeholders could mitigate the damaging
530 effects of extreme flooding by creating and managing resilient sites based upon individual
531 species that are best adapted to the particular flood scenarios predicted.

532

533 **Acknowledgements**

534 The authors thank the School of Environment and Technology at the University of Brighton
535 for funding this research. Thanks to Dr. Magda Grove, Christine Sinclair, Linda Barber and
536 Pete Mathers for technical support.

537

538 **References**

539 Araya, Y., Gowing, D. J., & Dise, N. (2010). A controlled water-table depth system to study
540 the influence of fine-scale differences in water regime for plant growth. *Aquatic Botany*, 92,
541 70–74. doi: 10.1016/j.aquabot.2009.10.004

542 Arnone, J. A. III., Jasoni, R. L., Lucchesi, J. A., Larsen, J. D., Leger, E. A., Sherry,
543 R.,... Verburg, P. S. J. (2011). A climatically extreme year has large impacts on C4 species in
544 tallgrass prairie ecosystems but only minor effects on species richness and other plant
545 functional groups. *Journal of Ecology*, 99, 678-688. doi:10.1111/j.1365-2745.2011.01813.x

546 Bailey-Serres, J., & Voesenek, L. A. C. J. (2008). Flooding stress: Acclimations and genetic
547 diversity. *Annual Review of Plant Biology*, 59, 313-339.
548 doi:10.1146/annurev.arplant.59.032607.092752

549 Bailey-Serres, J., & Voesenek, L. A. (2010). Life in the balance: a signalling network
550 controlling survival of flooding. *Current Opinion in Plant Biology*, 13, 489-494.
551 doi:10.1016/j.pbi.2010.08.002

552 Bailey, L. D., & van de Pol, M. (2016). Tackling extremes: challenges for ecological and
553 evolutionary research on extreme climatic events. *Journal of Animal Ecology*, 85, 85-96.
554 doi:10.1111/1365-2656.12451

555 Banach, K., Banach, A. M., Lamers, L. P. M., De Kroon, H., Bennicelli, R. P., Smits, A. J.
556 M., & Visser, E. J. W. (2009). Differences in flooding tolerance between species from two
557 wetland habitats with contrasting hydrology: implications for vegetation development in
558 future floodwater retention areas. *Annals of Botany*, 103, 341–351. doi:10.1093/aob/mcn183

559 Blom, C. W. P. M., Bögemann, G. M., Laan, P., van der Sman, A. J. M., van de Steeg, H. M.,
560 & Voesenek, L. A. C. J. (1990). Adaptations to flooding in plants from river areas. *Aquatic*
561 *Botany*, 38, 29-47.

562 Blöschl, G., Hall, J., Parajka, J., Perdigão, R. A. P., Merz, B., Arheimer, B.,...Živković, N.
563 (2017). Changing climate shifts timing of European floods. *Science*, 357, 588-590.
564 doi:10.1126/science.aan2506

565 Brotherton, S. J., & Joyce, C. B. (2015). Extreme climate events and wet grasslands: plant
566 traits for ecological resilience. *Hydrobiologia*, 750, 229-243. doi:10.1007/s10750-014-2129-5

567 Brotherton, S. J. (2017). Responses of floodplain grassland plants to extreme climate events:
568 survival, growth and flowering. PhD thesis. School of Environment and Technology,
569 University of Brighton, UK.

570 Campbell, D., Keddy, P. A., Broussard, M., & McFalls-Smith, T. B. (2016). Small changes in
571 flooding have large consequences: experimental data from ten wetland plants. *Wetlands*, 36,
572 457–466. doi:10.1007/s13157-016-0754-7

573 Casanova, M. T., & Brock, M. A. (2000). How do depth, duration and frequency of flooding
574 influence the establishment of wetland plant communities? *Plant Ecology*, 147, 237–250.
575 doi:10.1023/A:1009875226637

576 Cusell, C., Lamers, L. P. M., van Wirdum, G., & Kooijman, A. (2013). Impacts of water level
577 fluctuation on mesotrophic rich fens: acidification vs. eutrophication. *Journal of Applied*
578 *Ecology*, 50, 998–1009. doi:10.1111/1365-2664.12096

579 Durant, D., Tichit, M., Fritz, H., & Kernéis, E. (2008). Field occupancy by breeding lapwings
580 *Vanellus vanellus* and redshanks *Tringa totanus* in agricultural wet grasslands. *Agriculture,*
581 *Ecosystems and Environment*, 128, 146-150. doi:10.1016/j.agee.2008.05.013

582 Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M., & Collins, S. L. (2003). Productivity
583 responses to altered rainfall patterns in a C4-dominated grassland. *Oecologia*, 137, 245–251.
584 doi:10.1007/s00442-003-1331-3

585 Fitter, A. H., & Fitter, R. S. R. (2002). Rapid changes in flowering time in British plants.
586 *Science*, 296, 1689-1691. doi:10.1126/science.1071617

587 Garssen, A. G., Baattrup-Pedersen, A., Voesenek, L. A. C. J., Verhoeven, J. T. A., & Soons,
588 M. B. (2015). Riparian plant community responses to increased flooding: a meta-analysis.
589 *Global Change Biology*, 21, 2881-2890. doi:10.1111/gcb.12921

590 Gowing, D. J. G., Lawson, C. S., Youngs, E. G., Barber, K. R., Rodwell, J. S., Prosser, M.
591 V.,...Spoor, G. (2002). The water regime requirements and the response to hydrological

592 change of grassland plant communities. Cranfield University, Silsoe, UK: Department for
593 Environment, Food and Rural Affairs.

594 Grime, J. P., Hodgson, J. G., & Hunt, R. (1992). Comparative plant ecology: A functional
595 approach to common British species (2nd ed.). Kirkcudbrightshire, UK: Castlepoint Press.

596 Grimm, V., & Wissel, C. (1997). Babel, or the ecological stability discussions: an inventory
597 and analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109, 323-334.
598 doi:10.1007/s004420050090

599 He, J. B., Bögemann, G. M., Van de Steeg, H. M., Rijnders, J. G. H. M., Voeselek, L. A. C.
600 J., & Blom, C. W. P. M. (1999). Survival tactics of *Ranunculus* species in river floodplains.
601 *Oecologia*, 118, 1-8. doi:10.1007/s004420050696

602 Hill, M. O., Mountford, J. O., Roy, D. B., & Bunce, R. H. B. (1999). Ellenberg's indicator
603 values for British plants. ECOFACT Volume 2, Technical Annex. Huntingdon. UK: Institute
604 of Terrestrial Ecology (and DETR).

605 Hill, M. O., Preston, C. D., & Roy, D. B. (2004). PLANTATT - Attributes of British and Irish
606 plants: status, size, life history, geography and habitats. Huntingdon, UK: NERC Centre for
607 Ecology and Hydrology.

608 Hovenden, M. J., Wills, K. E., Vander Schoor, J. K., Williams, A. L., & Newton, P. C.
609 (2008). Flowering phenology in a species-rich temperate grassland is sensitive to warming
610 but not elevated CO₂. *New Phytologist*, 178, 815-822. doi:10.1111/j.1469-
611 8137.2008.02419.x

612 IPCC (2007) Climate change 2007: The physical science basis. In: Solomon S, Qin D,
613 Manning M et al (eds) Contribution of Working Group I to the Fourth Assessment Report of

614 the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University
615 Press.

616 Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-change
617 experiments: Events, not trends. *Frontiers in Ecology and the Environment*, 5, 365-374.
618 doi:10.1890/1540-9295(2007)5

619 Jentsch, A., Kreyling, J., Boettcher-Treschkow, J., & Beierkuhnlein, C. (2009). Beyond
620 gradual warming: Extreme weather events alter flower phenology of European grassland and
621 heath species. *Global Change Biology*, 15, 837-849. doi:10.1111/j.1365-2486.2008.01690.x

622 Jentsch, A., Kreyling, J., Elmer, M., Gellesch, E., Glaser, B., Grant, K.,...Beierkuhnlein C.
623 (2011). Climate extremes initiate ecosystem-regulating functions while maintaining
624 productivity. *Journal of Ecology*, 99, 689-702. doi:10.1111/j.1365-2745.2011.01817.x

625 Johansson, M. E., & Nilsson, C. (2002). Responses of riparian plants to flooding in free-
626 flowing and regulated boreal rivers: an experimental study. *Journal of Applied Ecology*, 39,
627 971–986. doi:10.1046/j.1365-2664.2002.00770.x

628 Joyce, C. B., Simpson, M., & Casanova, M. (2016). Future wet grasslands: ecological
629 implications of climate change. *Ecosystem Health and Sustainability*, 2, 1-15.
630 doi:10.1002/ehs2.1240

631 Kercher, S. M., & Zedler, J. B. (2004). Multiple disturbances accelerate invasion of reed
632 canary grass (*Phalaris arundinacea* L.) in a mesocosm study. *Oecologia*, 138, 455-464.
633 doi:10.1007/s00442-003-1453-7

634 Kreyling, J., Wenigmann, M., Beierkuhnlein, C., & Jentsch, A. (2008). Effects of extreme
635 weather events on plant productivity and tissue die-back are modified by community
636 composition. *Ecosystems*, 11, 752-763. doi:10.1007/s10021-008-9157-9

637 Kundzewicz, Z. W., Pińskwar, I., & Brakenridge, G. R. (2013). Large floods in Europe,
638 1985-2009. *Hydrological Sciences Journal*, 58, 1-7. doi:10.1080/02626667.2012.745082

639 Loeb, R., Lamers, L. P. M., & Roelofs, J. G. M. (2008). Effects of winter versus summer
640 flooding and subsequent desiccation on soil chemistry in a riverine hay meadow. *Geoderma*,
641 145, 84-90. doi:10.1016/j.geoderma.2008.02.009

642 Luo, W., Xiw, Y., Chen, X., & Li, F. (2010). Competition and facilitation in three marsh
643 plants in response to a water-level gradient. *Wetlands*, 30, 525-530. doi:10.1007/s13157-010-
644 0064-4

645 Mallakpour, I., & Villarini, G. (2015). The changing nature of flooding across the central
646 United States. *Nature Climate Change*, 5, 250-254. doi:10.1038/NCLIMATE2516

647 McKendrick, S. L. (1995). The effects of herbivory and vegetation on laboratory-raised
648 *Dactylorhiza praetermissa* (Orchidaceae) planted into grassland in Southern England.
649 *Biological Conservation*, 73, 215-220. doi:10.1016/0006-3207(94)00111-3

650 Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the
651 disruption of plant–pollinator interactions. *Ecology Letters*, 10, 710-717. doi:10.1111/j.1461-
652 0248.2007.01061.x

653 metoffice.co.uk. (2014). Winter 2013/14.
654 <http://www.metoffice.gov.uk/climate/uk/summaries/2014/winter>.

655 Mori, A. S. (2011). Ecosystem management based on natural disturbances: hierarchical
656 context and non-equilibrium paradigm. *Journal of Applied Ecology*, 48, 280-292.
657 doi:10.1111/j.1365-2664.2010.01956.x

658 Nielsen, D. L., Podnar, K., Watts, R. J., & Wilson, A. L. (2013). Empirical evidence linking
659 increased hydrologic stability with decreased biotic diversity within wetlands. *Hydrobiologia*,
660 708, 81-96. doi:10.1007/s10750-011-0989-5

661 Newbold, C., & Mountford, J. O. (1997). Water level requirements of wetland plants and
662 animals. Peterborough, UK: English Nature

663 Niu, S., Luo, Y., Li, D., Cao, S., Xia, J., Li, J., & Smith, M. D. (2014). Plant growth and
664 mortality under climatic extremes: an overview. *Environmental and Experimental Botany*,
665 98, 13-19. doi:10.1016/j.envexpbot.2013.10.004

666 Nygaard, B., & Ejrnæs, R. (2009). The impact of hydrology and nutrients on species
667 composition and richness: evidence from a microcosm experiment. *Wetlands*, 29, 187-195.
668 doi:10.1672/08-13.1

669 Osborne, J. W., & Overbay, A. (2004). The power of outliers (and why researchers should
670 always check for them). *Practical Assessment, Research and Evaluation*, 9. Available online:
671 <http://PAREonline.net/getvn.asp?v=9&n=6>.

672 Pierik, R., van Aken, J. M., & Voesenek, L. A. C. J. (2009). Is elongation-induced leaf
673 emergence beneficial for submerged *Rumex* species? *Annals of Botany*, 103, 353–357.
674 doi:10.1093/aob/mcn143

675 Price, M. V., & Waser, N. M. (1998). Effects of experimental warming on plant reproductive
676 phenology in a subalpine meadow. *Ecology*, 79, 1261–1271. doi:10.1890/0012-9658

677 Reyer, C. P. O., Leuzinger, S., Rammig, A., Wolf, A., Bartholomeus, R. P., Bonfante,
678 A.,...Pereira, M. (2013). A plant's perspective of extremes: terrestrial plant responses to
679 changing climatic variability. *Global Change Biology*, 19, 75–89. doi:10.1111/gcb.12023

680 Rodwell, J. S. (1991). *British Plant Communities. Volume 2. Mires and heath*. Cambridge,
681 UK: Cambridge University Press.

682 Rodwell, J. S. (1992). *British Plant Communities. Volume 3. Grasslands and montane*
683 *communities*. Cambridge, UK: Cambridge University Press.

684 Sherry, R. A., Zhou, X., Gu, S., Arnone, J. A., Schimel, D. S., Verburg, P. S.,...Luo Y.
685 (2007). Divergence of reproductive phenology under climate warming. *Proceedings of the*
686 *National Academy of Sciences*, 104, 198-202. doi:10.1073/pnas.0605642104

687 Silvertown, J., Dodd, M.E., Gowing, D.J.G., & Mountford, J.O. (1999). Hydrologically
688 defined niches reveal a basis for species richness in plant communities. *Nature*, 400, 61-63.

689 Smith, M. (2011). An ecological perspective on extreme climatic events: a synthetic
690 definition and framework to guide future research. *Journal of Ecology*, 99, 656–663.
691 doi:10.1111/j.1365-2745.2011.01798.x

692 Smith, R. G. B., & Brock, M. A. (1996). Coexistence of *Juncus articulatus* L. and *Glyceria*
693 *australis* C. E. Hubb in a temporary shallow wetland in Australia. *Hydrobiologia*, 340, 147-
694 151. doi:10.1007/BF00012747

695 Striker, G. G., Inausti, P., Grimaldi, A. A., & Vega, A. S. (2007). Trade-off between root
696 porosity and mechanical strength in species with different types of aerenchyma. *Plant, Cell*
697 *and Environment*, 30, 580–589. doi:10.1111/j.1365-3040.2007.01639.x

698 Striker, G. G., Mollard, F. P. O., Grimaldi, A. A., León, R. J. C., & Inausti, P. (2011).
699 Trampling enhances the dominance of graminoids over forbs in flooded grassland
700 mesocosms. *Applied Vegetation Science*, 14, 95-106. doi:10.1111/j.1654-109X.2010.01093.x

701 Tebaldi, C., Hayhoe, K., Arblaster, J., & Meehl, G. A. (2006). Going to Extremes: The
702 intercomparison of model-simulated historical and future changes in extreme events. *Climatic*
703 *Change*, 79, 185-211. doi:10.1007/s10584-006-9051-4

704 Thompson, R. M., Beardall, J., Beringer, J., Grace, M., & Sardina, P. (2013). Means and
705 extremes: building variability into community-level climate change experiments. *Ecology*
706 *Letters*, 16, 799–806. doi:10.1111/ele.12095

707 Toogood, S. E., & Joyce, C. B. (2009). Effects of raised water levels on wet grassland plant
708 communities. *Applied Vegetation Science*, 12, 283–294. doi:10.1111/j.1654-
709 109X.2009.01028.x

710 Toogood, S. E., Joyce, C. B., & Waite, S. (2008). Response of floodplain grassland plant
711 communities to altered water regimes. *Plant Ecology*, 197, 285-298. doi:10.1007/s11258-
712 007-9378-6

713 Toräng, P., Ehrlén, J., & Ågren, J. (2010). Habitat quality and among-population
714 differentiation in reproductive effort and flowering phenology in the perennial herb *Primula*
715 *farinosa*. *Evolutionary Ecology*, 24, 715–729. doi:10.1007/s10682-009-9327-z

716 Van der Kamp, G., Hayashi, M., Bedard-Haughn, A., & Pennock, D. (2016). Prairie pothole
717 wetlands – suggestions for practical and objective definitions and terminology. *Wetlands*, 36,
718 229-235. doi:10.1007/s13157-016-0809-9

719 Van Eck, W. H. J. M., van de Steeg, H. M., Blom, C. W. P. M., & de Kroon, H. (2004). Is
720 tolerance to summer flooding correlated with distribution patterns in river floodplains? A
721 comparative study of 20 terrestrial grassland species. *Oikos*, 107, 393-405.
722 doi:10.1111/j.0030-1299.2004.13083.x

723 Van Eck, W. H. J. M., Lenssen, J. P., van de Steeg, H. M., Blom, C. W. P. M., & de Kroon,
724 H. (2006). Seasonal dependent effects of flooding on plant species survival and zonation: a
725 comparative study of 10 terrestrial grassland species. *Hydrobiologia*, 565, 59-69.
726 doi:10.1007/s10750-005-1905-7

727 Van der Sman, A. J. M., Voeselek, L. A. C. J., Blom, C. W. P. M., Harren, F. J. M., &
728 Reuss, J. (1991). The role of ethylene in shoot elongation with respect to survival and seed
729 output of flooded *Rumex maritimus* L. plants. *Functional Ecology*, 5, 304-313.
730 doi:10.2307/2389269

731 Vervuren, P. J. A., Blom, C. W. P. M., & de Kroon, H. (2003). Extreme flooding events on
732 the Rhine and the survival and distribution of riparian plant species. *Journal of Ecology*, 91,
733 135-146. doi:10.1046/j.1365-2745.2003.00749.x

734 Watson, E. B., Wigand, C., Cencer, M., & Blount, K. (2015). Inundation and precipitation
735 effects on growth and flowering of the high marsh species *Juncus gerardii*. *Aquatic Botany*,
736 121, 52-56. doi.org/10.1016/j.aquabot.2014.10.012

737 Weiher, E., & Keddy, P. A. (1995). The assembly of experimental wetland plant
738 communities. *Oikos*, 73, 323-335. doi:10.2307/3545956

739 Winter, T. C., & Rosenberg, D. O. (1998). Hydrology of prairie pothole wetlands during
740 drought and deluge: A 17-year study of the Cottonwood Lake wetland complex in North
741 Dakota in the perspective of longer term measured and proxy hydrological records. *Climatic
742 Change*, 40, 189-209.

743 Wright, A. J., de Kroon, H., Visser, E. J. W., Buchmann, T., Ebeling, A., Eisenhauer,
744 N.,...Liesje, M. (2017). Plants are less negatively affected by flooding when growing in
745 species-rich plant communities. *New Phytologist*, 213, 645-656. doi:10.1111/nph.14185

746 Yetisir, H., Çaliskan, M. E., Soylu, S., & Sakar, M. (2006). Some physiological and growth
747 responses of watermelon [*Citrullus lanatus* (Thunb.) Matsum. and Nakai] grafted onto
748 *Lagenaria siceraria* to flooding. *Environmental and Experimental Botany*, 58, 1–8.
749 doi:10.1016/j.envexpbot.2005.06.010

750

751 **Table 1** Summary of functional traits and habitat preferences for the four species used in the experiment

| Experimental classification | Species name | Ellenberg IV ¹ | | | Life history ² | Life form | Water level preference ³ | Habitat preference ⁴ | Global distribution ⁴ |
|-----------------------------|-----------------------------------|---------------------------|---|---|---------------------------|---------------------|-------------------------------------|---|---|
| | | F | L | N | | | | | |
| Hydric | <i>Cardamine pratensis</i> | 8 | 7 | 4 | C-S-R/R | Perennial forb | -5 - +5 cm | Wet grasslands, wet woodlands | Europe, Western Asia, North America |
| Hydric | <i>Juncus articulatus</i> | 9 | 8 | 3 | C-R/C-S-R | Perennial graminoid | -30 - 0 cm | Wet grasslands, mires, wet woodlands, dune slacks | Northern hemisphere (introduced in Southern hemisphere) |
| Mesic | <i>Ranunculus acris</i> | 6 | 7 | 4 | C-S-R | Perennial forb | Not known | Unimproved meadows, agricultural and amenity grasslands | Europe and Asia (widely introduced elsewhere) |
| Mesic | <i>Scorzonerooides autumnalis</i> | 6 | 8 | 4 | C-S-R/R | Perennial forb | Not known | Amenity and agricultural grasslands, open habitats | Eurasia (introduced to North America) |

752 ¹ Hill, Mountford, Roy, and Bunce (1999), Indicator Values (IV) are F= moisture (1= extreme dryness – 12= submerged), L= light (1= deep

753 shade – 9= full light), N= nitrogen (1= extremely infertile – 9= extremely rich)

754 ²Grime, Hodgson, and Hunt (1992), C= competitor, S= stress tolerator, R= ruderal

755 ³Newbold and Mountford (1997)

757 **Figure 1** Mean (± 1 SE) maximum leaf length during the experiment per species by flooding
758 treatment. For each date tested, values that do not differ significantly ($P < 0.05$ with
759 Bonferroni correction, Linear Mixed-Effects Modelling, Least Significant Difference) have a
760 letter (A, B or C) in common. $n = 18$ except *C. pratensis* control mid and end dates, and *J.*
761 *articulatus* 7-day flood end date, where $n = 17$

762 **Figure 2** Mean number (± 1 SE) of flowering stems per flowering plant by species and
763 treatment. For each species, values that do not differ significantly ($P < 0.05$ with Bonferroni
764 correction, Generalized Linear Modelling, Least Significant Difference) have a letter (A or B)
765 in common. The outcome of the test is shown only if significant treatment difference was
766 observed

767 **Figure 3** Mean (± 1 SE) maximum flowering stem height per flowering plant by species and
768 treatment. Data for one outlier *R. acris* plant was removed in the 2-day flood treatment. For
769 each species, values that do not differ significantly ($P < 0.05$, ANOVA, Tukeys test) have a
770 letter (A or B) in common. The outcome of the test is shown only if significant treatment
771 difference was observed

772 **Figure 4** Mean number (± 1 SE) of flowers per flowering plant by species and treatment. One
773 outlier plant was removed for *R. acris* in the 2-day flood treatment. *J. articulatus* values are
774 for flowering stems. For each species, values that do not differ significantly ($P < 0.05$ with
775 Bonferroni correction, Generalized Linear Modelling, Least Significant Difference) have a
776 letter (A or B) in common. The outcome of the test is shown only if significant treatment
777 difference was observed

778 **Figure 5** Earliest day at which each phenological stage was recorded per species by any
779 plant within that treatment. Day 65= 6-Mar and 230= 18-Aug. S1 - Unopened buds; S2 -
780 Open flowers; S3 - Old flowers defined as postanthesis; S4 - Petals gone and initial fruit; S5 -

781 Expanded fruit; and S6 - Dehisced fruit (after Price & Waser, 1998). Stages 3 and 5 were not
782 recorded for *S. autumnalis* in the 7-day flood treatment because they occurred between
783 sampling dates. Stage 3 was not observed for *J. articulatus*

784 **Figure 6** Days when percentiles of plants supported open flowers (phenological stage S2 after
785 Price & Waser, 1998) per species and treatment. The bars represent $\geq 25\%$ - $\leq 75\%$ of plants
786 in open flower; the diamond symbol represents $\geq 50\%$ of plants in open flower

787

788 **Supporting information**

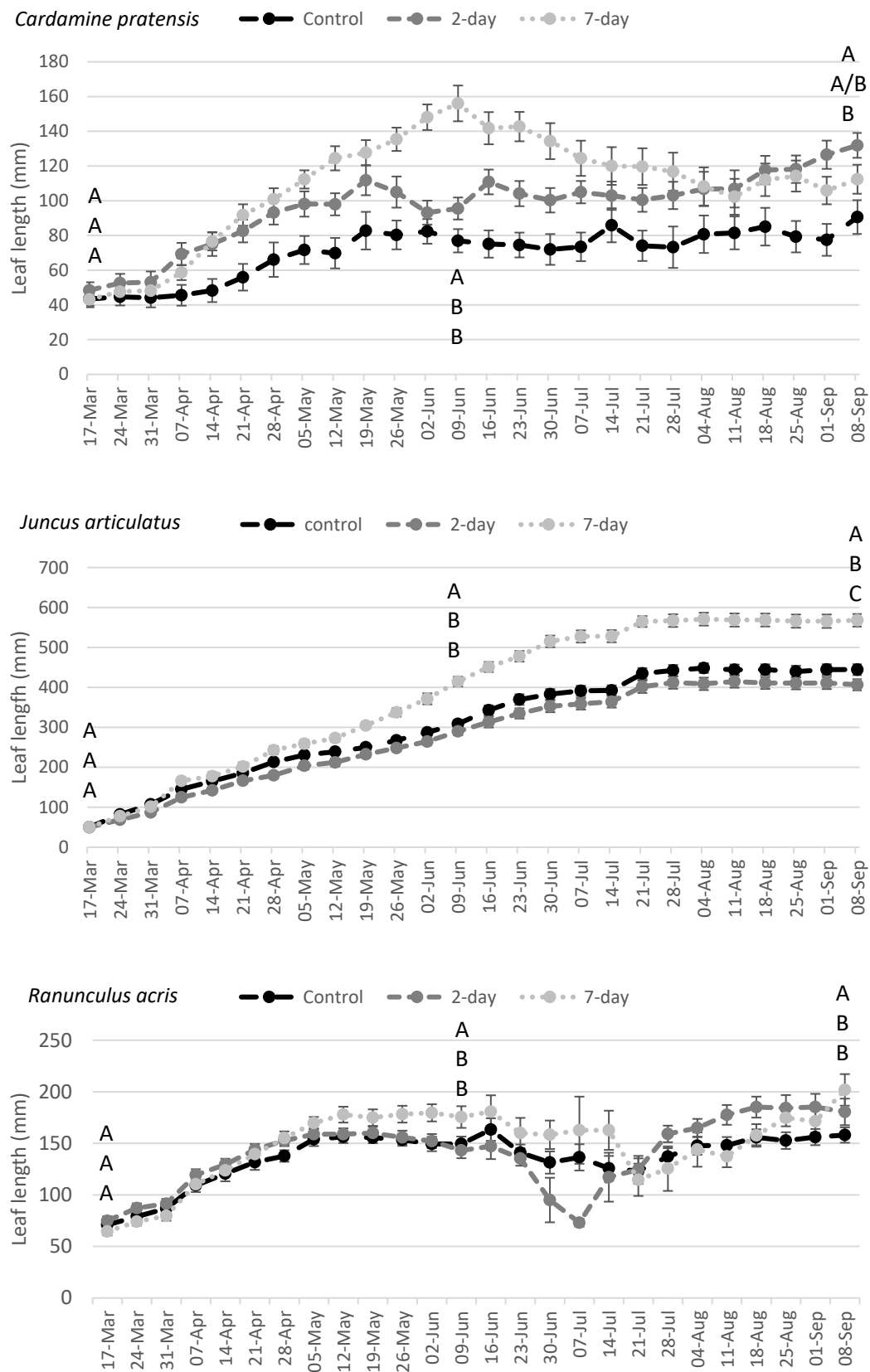
789 **Table S-1** Results of the Linear Mixed-Effects Modelling for repeated measurements of
790 maximum leaf length per species by treatment and time. Bonferroni corrected significance for
791 $P = 0.006$

792 **Table S-2** Results of the Generalized Linear Models for flowering stem abundance per
793 flowering plant per species. Bonferroni corrected significance for $P = 0.017$

794 **Table S-3** Results of one-way ANOVA for maximum flowering stem height per flowering
795 plant per species

796 **Table S-4** Results of the Generalized Linear Models for the number of flowers per flowering
797 plant per species. Bonferroni corrected significance for $P = 0.017$

Fig. 1



Scorzoneroides autumnalis

—●— control -●- 2-day ····●···· 7-day

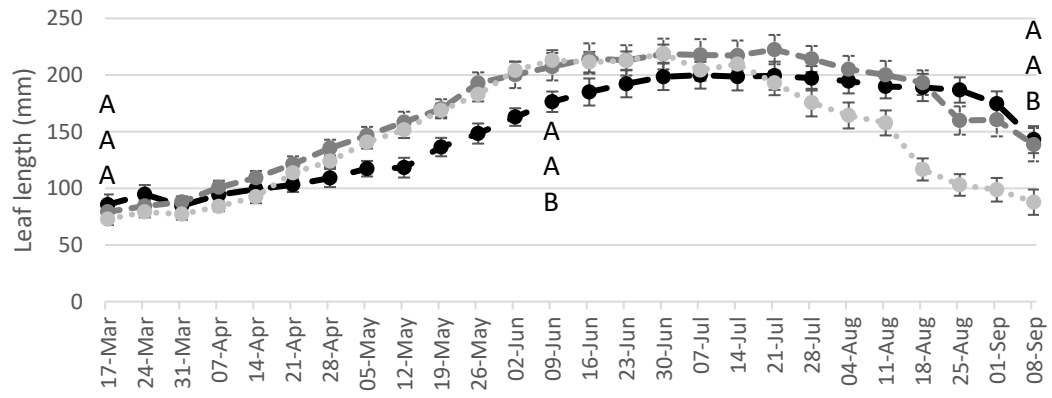


Fig. 2

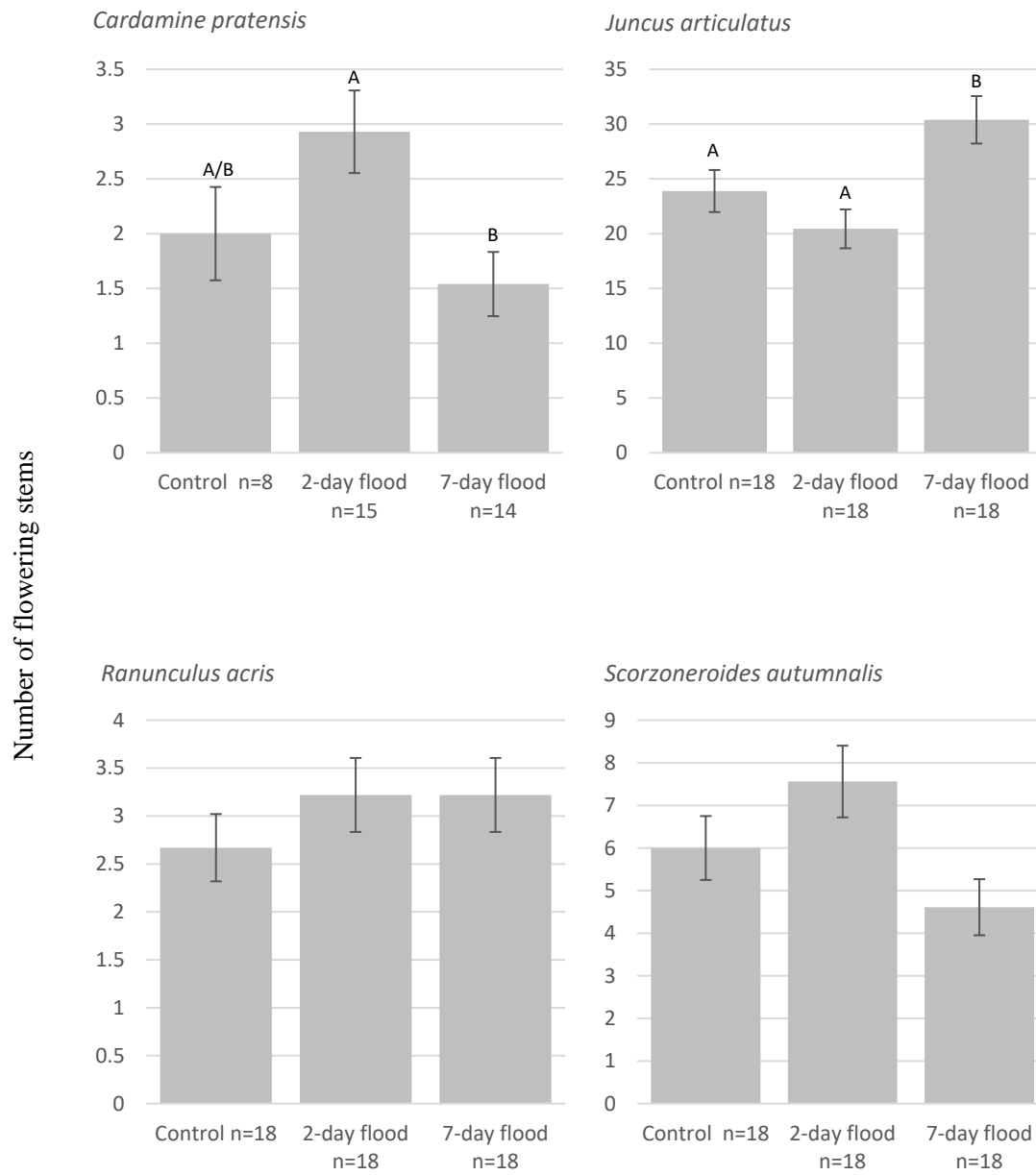


Fig. 3

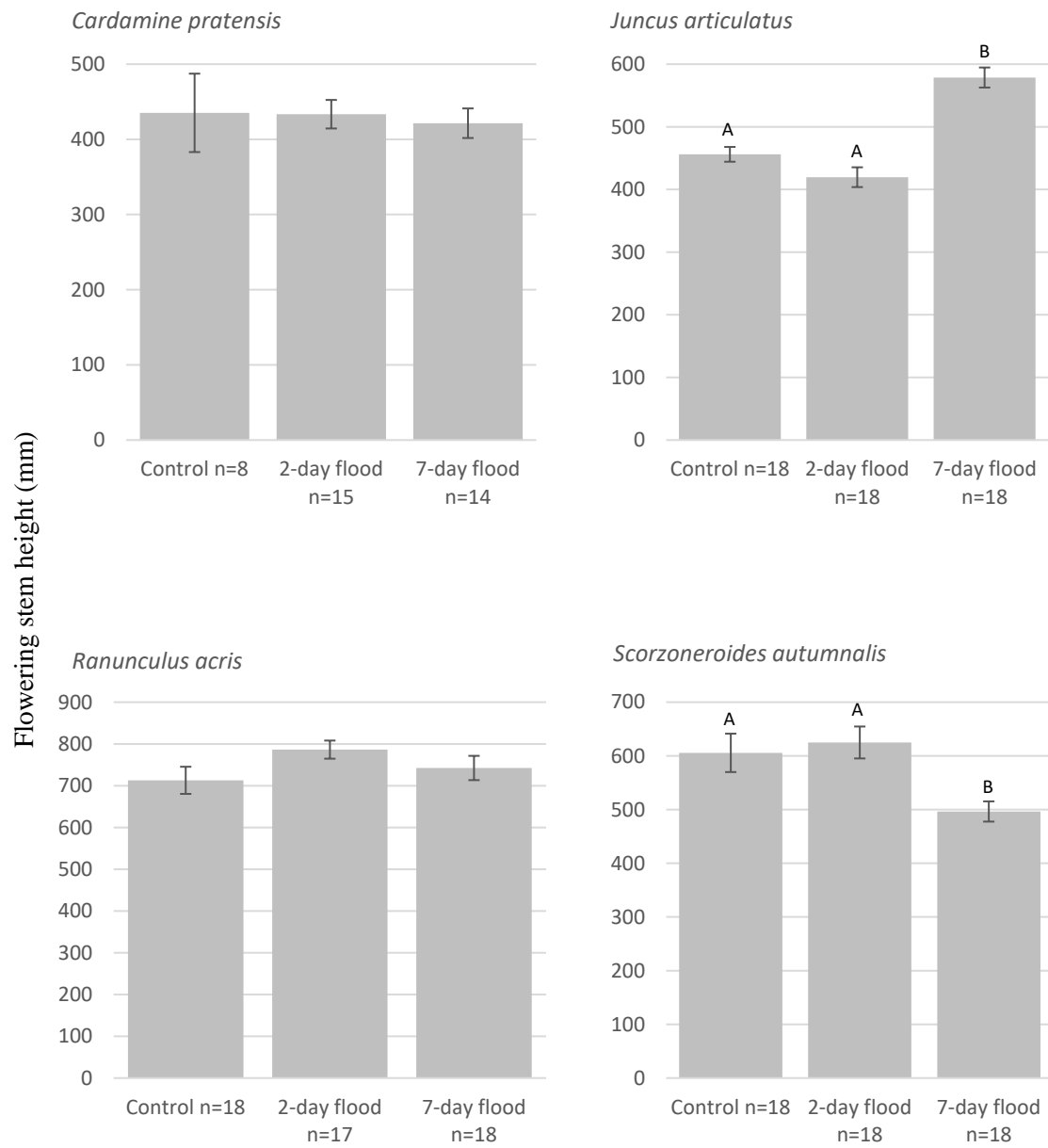


Fig. 4

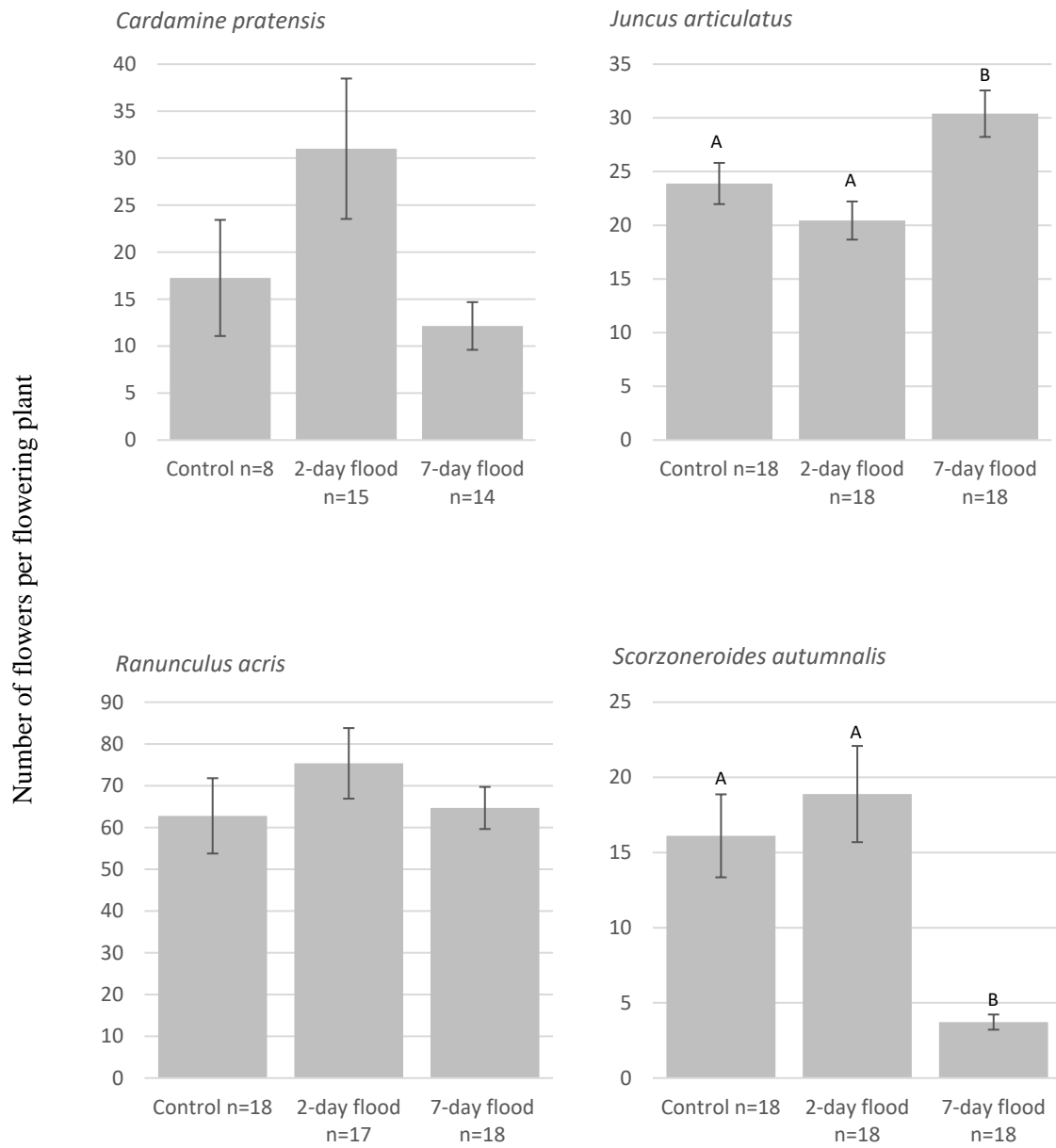
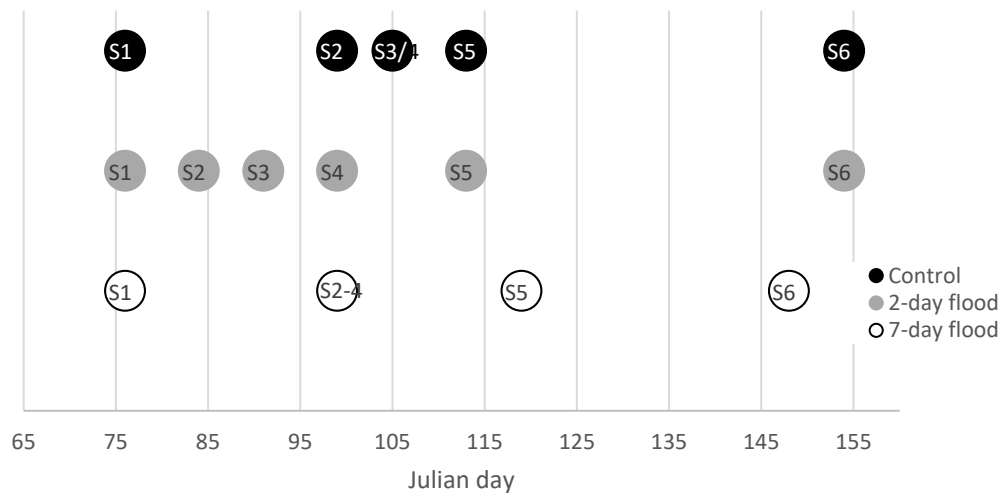
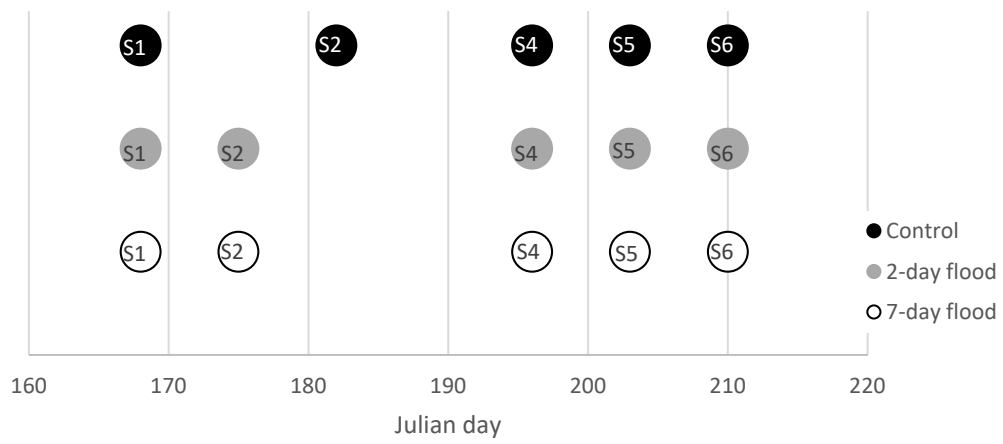


Fig. 5

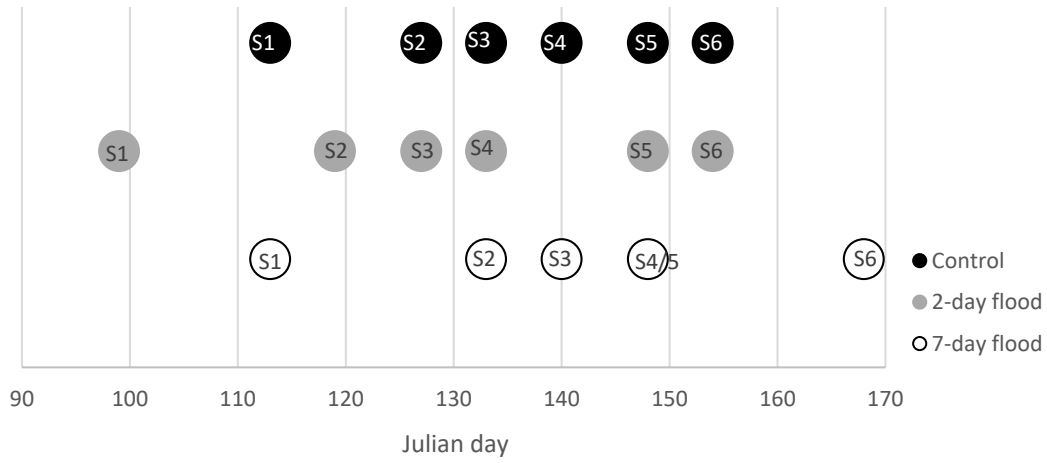
Cardamine pratensis



Juncus articulatus



Ranunculus acris



Scorzoneroides autumnalis

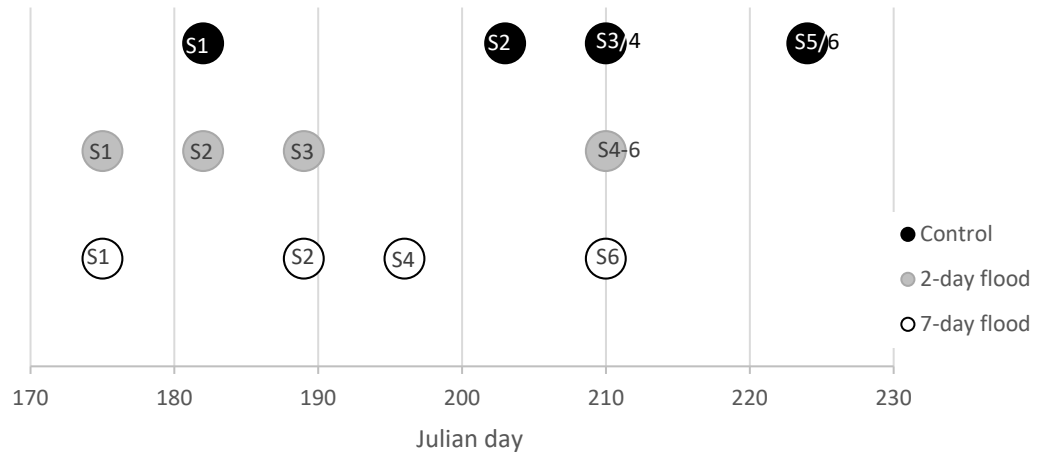


Fig. 6

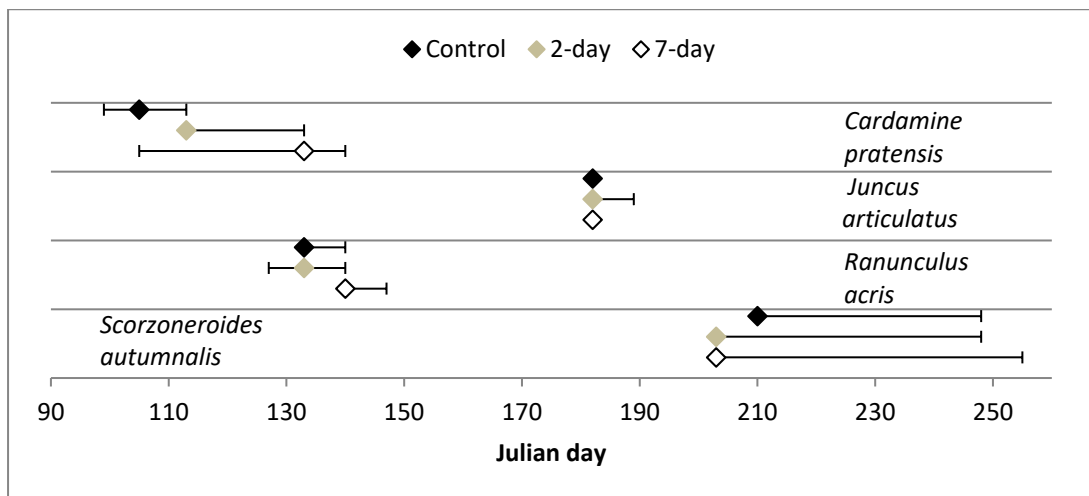
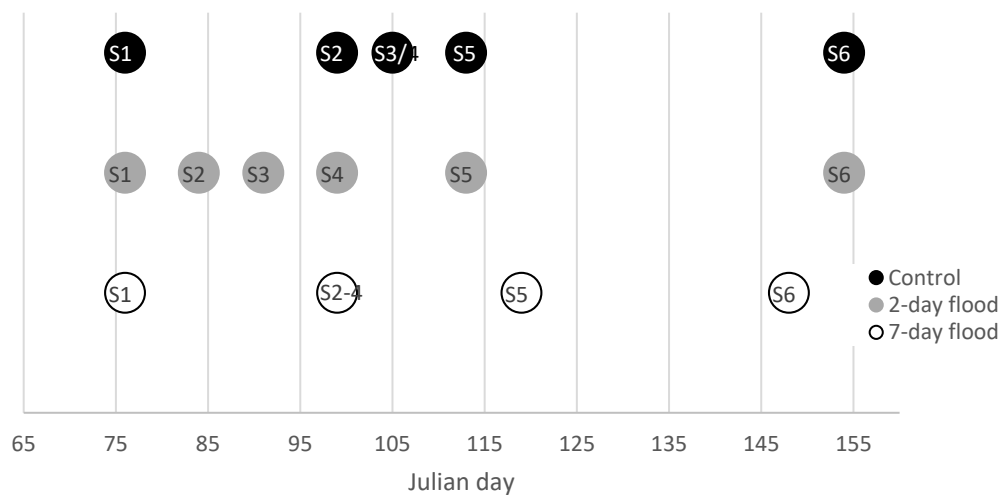
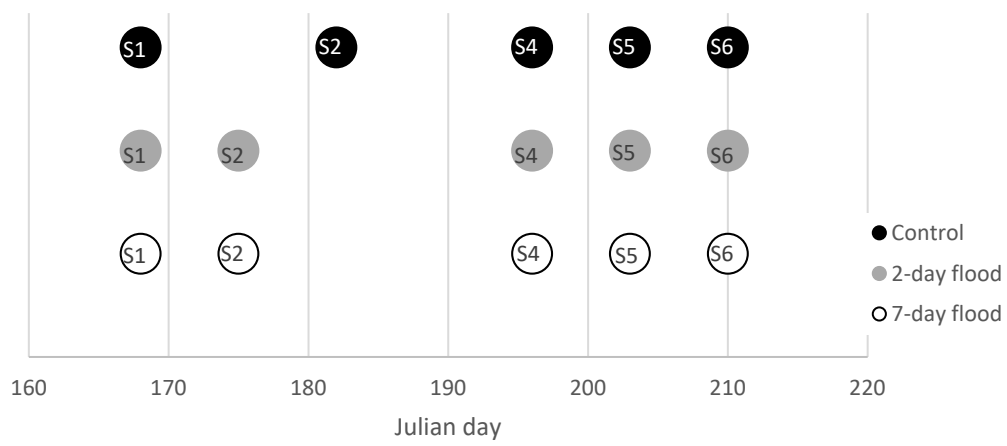


Fig. 5

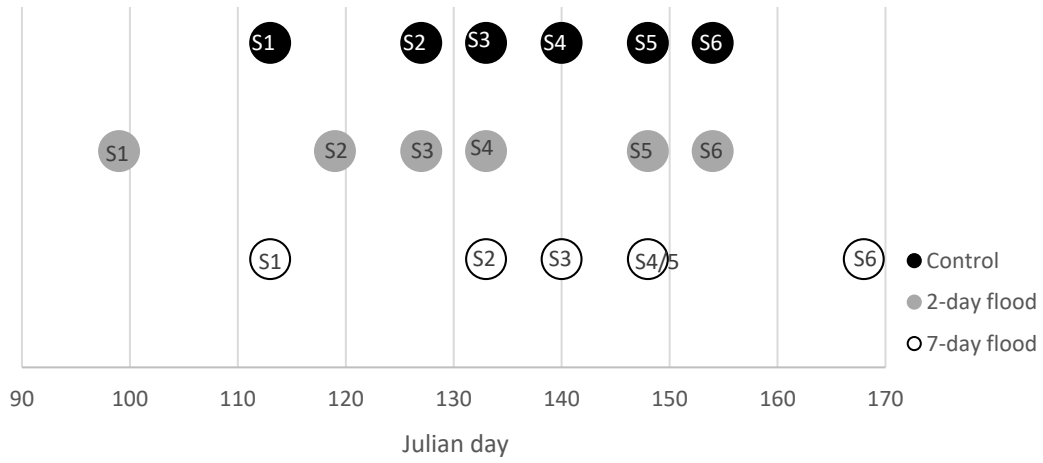
Cardamine pratensis



Juncus articulatus



Ranunculus acris



Scorzoneroides autumnalis

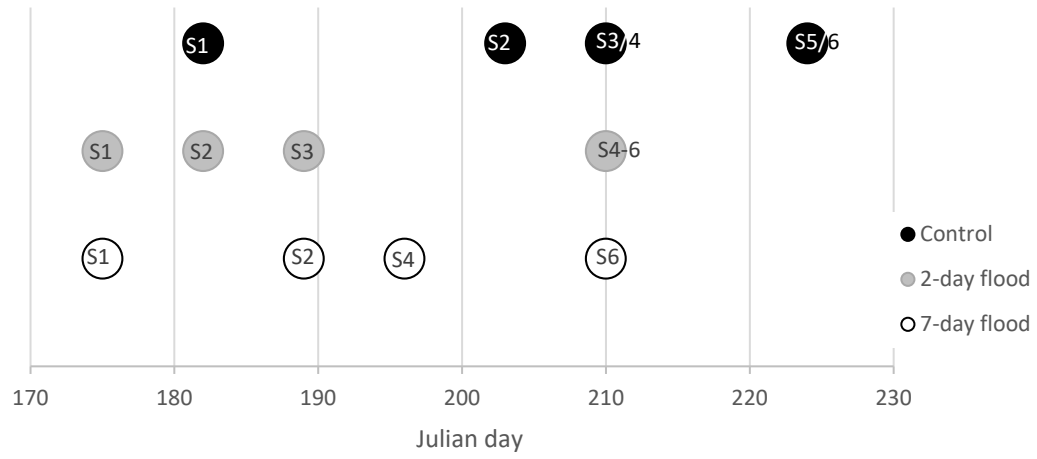


Fig. 6

