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3 **Facilitative and competitive effects of a large species with defensive traits on a**
4 **grazing-adapted, small species in a long-term deer grazing habitat**

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19 Running headline: Interactions between two grazing-adapted species

20

1 **Abstract**

2 Plants can adapt to grazing environments by developing defensive traits, such as spines and
3 toxins, or having a small phenotype, such as short and prostrate growth forms. This study
4 examined facilitative and competitive interactions between species with different types of
5 grazing adaptation. We predicted that large species with defensive traits sometimes protect
6 grazing-adapted species without defensive traits from herbivores, but competitively suppress
7 them overall. We conducted an experiment using fences and removals of an unpalatable plant
8 in the long-term deer grazing habitat of Nara Park in Nara, Japan. We evaluated the seasonal
9 variations in the facilitative and competitive effects of a defensive perennial, *Urtica*
10 *thunbergiana*, on the growth, survival, reproduction, and final fitness of a small palatable
11 annual species, *Persicaria longiseta*, during a growing season. The populations of the two
12 species in the park have adapted to the grazed habitat by increasing the density of stinging hairs
13 (*Urtica*) and developing inherently short shoots and small leaves (*Persicaria*). We found that
14 *Urtica* individuals had facilitative effects on the growth of *Persicaria* individuals under grazing
15 during a few periods of the growing season, but had neutral effects on survival and plant fitness
16 throughout the season. In the fenced plots, *Urtica* had negative effects on the growth, survival,
17 and reproduction of *Persicaria*. These results suggest that the relative importance of the
18 facilitative and competitive effects of *Urtica* on *Persicaria* fluctuated due to seasonal variations
19 in grazing pressure and vegetative productivity. Although well-defended plants often facilitate
20 less-defended species, we conclude that the facilitative effects of *Urtica* on *Persicaria* are
21 limited in a plant community with a long history of intensive grazing.

22

23 **Key words:** competition, deer grazing, facilitation, grazing-adapted, *Persicaria longiseta*,

1 seasonal variation, *Urtica thunbergiana*

2

1 **INTRODUCTION**

2 Unpalatable species often protect their small palatable neighboring plants from grazers
3 through their upper canopy cover, thus facilitating the performance of small plants lacking
4 defense mechanisms under grazing pressure (Russell and Fowler 2004; Bossuyt et al. 2005;
5 Callaway et al. 2005; Baraza et al. 2006). In grazing habitats, the positive effects of unpalatable
6 species enhance local species diversity and productivity of plants in areas around them
7 (Callaway et al. 2000). Thus, indirect positive interactions play an important role in structuring
8 grazed plant communities (Manier and Hobbs 2006; Osem et al. 2007), and the conservation of
9 these natural grazing refuges is essential for maintaining the biodiversity of grassland flora
10 (reviewed in Milchunas and Noy-Meir 2002).

11 Large unpalatable plants can also competitively suppress small palatable neighbors.
12 Many previous studies have assessed the relative importance of facilitative and competitive
13 effects, and the net effects of unpalatable plants in grazing habitats (Callaway et al. 2005; Graff
14 et al. 2007; Osem et al. 2007; Levenbach 2009), but the majority of those studies measured the
15 results of these effects at the end of the growing season. The relative importance of competitive
16 and facilitative effects may vary with seasonal variations in grazing pressure (Alberti et al.
17 2008) and abiotic stress (Veblen 2008). Facilitative effects can also differentially affect plant
18 performance traits (growth, survival, reproduction) in palatable species, such that palatable
19 species with unpalatable neighbors may have increased survival but reduced growth and
20 reproduction due to competition with their large neighbours (Smit et al. 2006).

21 Several previous studies have provided evidence that unpalatable plants can protect very
22 palatable plants that could not survive or grow without protection from grazing. Few studies
23 have examined interactions between species adapted to grazed habitats in different ways

1 (Callaway et al. 2005; Baraza et al. 2006; Vandenberghe et al. 2009). A long evolutionary
2 history of grazing by large ungulates often selects for genotypes or plant species that develop
3 short stature and prostrate growth forms (Warwick and Briggs 1980; Detling and Painter 1983;
4 McNaughton 1984; Polley and Detling 1988; McKinney and Fowler 1991; Dorrough et al.
5 2004; Ishikawa et al. 2006). Relative to large plants that possess longer stems and larger leaves,
6 small plants can minimize grazer access to aboveground parts and achieve rapid regrowth after
7 grazing (Rosenthal and Kotanen 1994; McIntyre and Lavorel 2001). However, small plants
8 also have reduced competitive ability for light (Briske and Anderson 1992; Hartvigsen and
9 McNaughton 1995; Osem et al. 2004; McGuire and Agrawal 2005). No studies, however, had
10 examined the facilitative and competitive effects of large unpalatable species with defensive
11 traits on a palatable species possessing small forms as a local adaptation to grazing habitats.

12 This study sought to examine the facilitative and competitive effects of a large species
13 with defensive traits on the growth, survival, reproduction, and final fitness of a
14 grazing-adapted, small species with no defensive traits, and the seasonal variations in these
15 effects during a growing season. We used a field experiment combining two treatments: the
16 establishment of exclosures and the experimental removal of defensive plants. We measured
17 interactions between an annual species, *Persicaria longiseta* (De Bruyn) Kitag., and a perennial
18 species, *Urtica thunbergiana* Siebold et Zucc., inhabiting Nara Park, Japan, in which a dense
19 population of sika deer *Cervus nippon* has long persisted. The population of *Persicaria* in Nara
20 Park is an ecotype that exhibits an inherently dwarf morphology with short shoots and small
21 leaves (Suzuki 2008). The population of *Urtica* in the park has evolved defensive traits by
22 increasing the density of stinging hairs, which are effective in reducing grazing damage and
23 increasing the survival of *Urtica* individuals in the park (Kato et al. 2008).

1 We predicted that *Urtica* plants have facilitative effects on some performance traits of
2 *Persicaria* plants during the growing season, but their total effects on *Persicaria* fitness are
3 neutral or even negative, because these plants with small forms suffer competitive pressure
4 from the large *Urtica* plants. Thus, as a logical consequence, we assumed that *Urtica* plants
5 have severe competitive effects on *Persicaria* plants inside fences where they are released from
6 deer grazing.

7

8 **MATERIALS AND METHODS**

9 The experiments were conducted at Nara Park (34°41' N, 135°50' E) at the eastern edge of Nara
10 Prefecture, western Japan. Annual mean precipitation is 1333 mm, and monthly mean
11 temperatures range from 3.8°C in January to 26.6°C in August in this region. The park is 660 ha
12 in area and includes open grasslands and evergreen forests. Sika deer (*Cervus nippon*
13 Temminck) populations have been distributed in this park for more than 1200 years, as they are
14 protected for religious reasons. During the late decade, the population density of deer has
15 reached extremely high levels (ca. 900 individuals / km² in flatland areas of the park;
16 Foundation for the Protection of Deer in Nara Park, 2006). The study sites were established in
17 a shady-moist environment in the understory of Japanese cedars that were sparsely planted,
18 where there were high densities of *Urtica* and *Persicaria* individuals in the park.
19 We examined the interactions between a palatable species, *Persicaria longiseta*, and an
20 unpalatable species, *Urtica thunbergiana*. *Persicaria longiseta* is an annual herb that is
21 distributed widely throughout East Asia and is common to roadsides, farms, edges of rice fields,
22 and gardens in Japan. Seed germination occurs primarily from the end of March to April.
23 During the growing season, plants form a number of lateral shoots from axillary buds proximal

1 to the base. Flowering is initiated in July. Reproductive plants produce a large number of small
2 seeds (*ca.* 1.5 mg per seed) but do not regenerate vegetatively. Fruit maturation and seed
3 dispersal occur from July to December, and seeds are dispersed by gravity as soon as they
4 mature. After reproduction, the plant dies by mid December. The population of *Persicaria* in
5 Nara Park is an ecotype adapted to grazing environments and exhibits inherently dwarf
6 morphology with shorter shoots and smaller leaves compared to populations with no grazing
7 history (Suzuki 2008).

8 The nettle *Urtica thunbergiana* is a perennial herb distributed within forest understories
9 throughout central and southern Japan. This species possesses stinging hairs containing toxins
10 on its stems and both surfaces of leaves; thus, they are unpalatable to deer because of these
11 physical and chemical defences (Kato et al. 2008). During a growing season, plants develop a
12 number of shoots proximal to the base. Most aboveground parts wither during the winter
13 season (Dec.–Mar.). The population of *U. thunbergiana* in Nara Park has evolved a much
14 higher density of stinging hairs compared to those in ungrazed areas as a consequence of local
15 adaptation to heavy grazing in the park (Kato et al. 2008).

16

17 ***Field experiment***

18 We used two experimental treatments, the establishment of exclosures and experimental
19 removal of the *Urtica* plants, to measure the effects of both competition and facilitation by
20 *Urtica* on neighbouring *Persicaria* under field conditions.

21 In July 2006, we established 40 plots of 50 × 50 cm in area with an *Urtica* individual
22 positioning at the center. We then drove metal stakes into the ground at each corner of the plots.
23 To examine the effects of *Urtica* with and without the effects of herbivory, we applied four

1 experimental treatments; *Urtica* present with and without fences (hereafter, referred to as F+U+
2 and F-U+, respectively), and *Urtica* removed with and without fences (hereafter, referred to as
3 F+U- and F-U-, respectively). Half of the 40 plots were fenced using 3-cm mesh wire net
4 (each fence: 0.5 × 0.5 × 0.5 m). The tops of fences were also covered with wire net to further
5 prevent deer from grazing plants within the fences. Because we used wire net with a large mesh
6 size, we assumed that the wire net did not affect physical conditions such as light and water
7 within the fences. We randomly chose 10 fenced and 10 unfenced plots and removed *Urtica*
8 individuals in the plots by cutting plants at the base. Most of these plants did not die when cut,
9 but any regrowth was cut at each census.

10 In 2007, we monitored *Persicaria* individuals establishing within the 40 study plots. All
11 plants in the plots were mapped, and the fate and size of each plant were recorded on 28
12 Apr.–24 May, 4–9 Jul., 12–13 Sep., and 24–26 Oct. 2007. In October, the number of flowers of
13 each plant was also counted. To quantify plant size, we measured the maximum length and the
14 perpendicular (D_1 and D_2 , respectively) of area covered by aboveground parts of each plant at
15 each census. As a measure of plant size, we calculated the area covered by each plant ($D_1 \times D_2$).
16 Lifetime fitness of each plant was estimated as the number of flowers produced by the plant
17 multiplied by the survival rate of plants in the treatment to which the plant belonged. The
18 survival rate of plants in each treatment was calculated as the number of surviving plants at the
19 end of study periods divided by the number of plants established in the plots of each treatment.
20 Relative growth rate (RGR) of each plant was calculated as plant size at a particular census
21 divided by plant size at the previous census.

22 We also monitored *Urtica* individuals in the study plots. All *Urtica* plants were mapped,
23 and the fate, height, and size of each plant were recorded at each census. The plant size of

1 *Urtica* individuals was quantified using the same method as with *Persicaria* individuals.

2

3 ***Analysis***

4 Data analysis was conducted using R (ver. 2.6.2.; R Development Core Team 2008). We used
5 generalized linear mixed-effects models (GLMMs) because our design included both fixed and
6 random effects, and our responses included variables with normal and non-normal error
7 distributions. After log-transformation, plant size, relative growth rate (RGR), number of
8 flowers, and fitness were analyzed with normal error distribution. Plant mortality was analyzed
9 with a binomial error distribution. The fence and *Urtica* treatments were treated as fixed
10 effects, and plots were treated as random effects. All GLMM analyses were conducted using
11 restricted maximum likelihood estimation, with the lmer function from the lme4 library in R.

12 Confidence intervals for each parameter estimate from the fitted GLMM were estimated
13 using Markov Chain Monte Carlo (MCMC) methods, with the mcmcsmpl function in R
14 (10,000 iterations). We calculated 95% confidence intervals using the HPDinterval function in
15 R. In this paper, we present estimates of the means from the MCMC and confidence intervals
16 of the estimated means to indicate least significant differences among treatments at $P = 0.05$
17 (treatments with non-overlapping intervals are significantly different). These MCMC methods
18 followed the analytical methods used in Hautier et al. (2009).

19

20 **RESULTS**

21 The initial number of *Persicaria* individuals was highest in F–U– and lowest in F+U+ (Table 1),
22 which may suggest that large *Urtica* plants in the F+U+ plots suppressed seedling
23 establishment of *Persicaria* under their canopy. Survival rates of *Persicaria* throughout a

1 growing season were 0.65 in F+U-, 0.37 in F+U+, 0.29 in F-U-, and 0.24 in F-U+,
2 respectively. The sizes of *Urtica* individuals tended to be higher in F+U+ than these in F-U+
3 throughout the season because a part of *Urtica* individuals was grazed in unfenced plots (Table
4 1). Although aboveground parts of *Urtica* were removed by cutting them at each census in
5 F-U- and F+U-, most of *Urtica* plants regrew in those plots (Table 1).

6 We found interactive effects of *Urtica* individuals and experimental protection from
7 grazing by fences on the performance of *Persicaria* individuals. In general, *Urtica* individuals
8 negatively affected the performances (growth, survival, and reproduction) of *Persicaria*
9 individuals in fenced plots, whereas they had either positive or neutral effects on *Persicaria* in
10 unfenced plots. A similar trend was observed across the study season.

11 In May, September, and October, the plant sizes of *Persicaria* in F-U+ were larger
12 compared to those in F-U-, whereas plant sizes in F+U+ tended to be smaller than those in
13 F+U- (Fig. 1). Of these differences, differences between F-U+ and F-U- in May and between
14 F+U+ and F+U- in October were statistically significant (Fig. 1). In July, the plant sizes of
15 *Persicaria* were smaller in plots with *Urtica* compared to those without *Urtica* in both of fenced
16 and unfenced plots, the difference between F+U+ and F+U- was statistically significant (Fig.
17 1).

18 The RGRs of *Persicaria* in F+U+ tended to be smaller than those in F+U- in all periods,
19 and the difference was significant during September–October (Fig. 2). In unfenced plots, the
20 RGRs of *Persicaria* were also significantly smaller in F-U+ than F-U- during May–July.
21 However, the RGRs were significantly larger in F-U+ than F-U- during September–October
22 (Fig. 2), which was opposite to the pattern observed in fenced plots during the same period.

23 The survival rates of *Persicaria* in F+U+ were also tended to be smaller than F+U- in all

1 periods, although these differences were not significant (Fig. 3). The survival rates of
2 *Persicaria* were very similar between F–U+ and F–U– (Fig. 3).

3 Individuals of *Persicaria* in F+U– produced the greatest number of flowers and attained
4 the highest fitness among treatments (466 % and 981 % of the means of the other three
5 treatments; Fig. 4). The differences were statistically significant. Individuals of *Persicaria* in
6 F+U+ produced the least number of flowers and the lowest fitness in all treatments, although
7 these traits did not significantly differ from those in F–U+ and F–U– (Fig. 4).

8 Overall, the presence of fences enhanced the growth, survival, and reproductive output
9 of *Persicaria* except for the growth during May–July, and the positive effects of fences were
10 more pronounced later in the season (Figs. 1–4).

11

12 **DISCUSSION**

13 We found interactive effects of *Urtica* individuals and experimental protection from
14 grazing by fences on the performance of *Persicaria* individuals. In general, *Urtica* individuals
15 negatively affected the growth, survival, and reproduction of *Persicaria* individuals in fenced
16 plots. In unfenced plots, they had positive effects on the size in May and relative growth rate
17 (RGR) in September–October, and a neutral effect on the survival and reproduction of
18 *Persicaria* throughout the growing season. In fenced plots released from grazing, all
19 performance traits of *Persicaria* increased compared to those in unfenced plots, suggesting that
20 they were grazed intensively under natural conditions. The negative effects of *Urtica* on
21 *Persicaria* in the fenced plots in all periods suggested that *Urtica* individuals competitively
22 suppressed their small neighbors throughout the growing season.

23 The net neutral effects of *Urtica* plants in unfenced plots likely resulted from the

1 combined effects of decreased competitive pressure of *Urtica* on *Persicaria*, and a balancing of
2 competition and facilitation in the grazed habitat. Competitive effects of *Urtica* on *Persicaria*
3 might have been relatively weak in unfenced plots compared to those in fenced plots because
4 the sizes of *Urtica* were reduced in unfenced plots possibly due to deer grazing. On the other
5 hand, *Persicaria* plants with small growth forms are likely competitively inferior to their larger
6 neighbors, and consequently, this increased the relative importance of competitive effects and
7 decreased the facilitative effects of *Urtica*. As described above, facilitative effects of *Urtica*
8 were observed only during part of the growing season. Therefore, we conclude that
9 competitive and facilitative effects of *Urtica* on *Persicaria* would have operated
10 simultaneously at a weak level, and that the competitive effects have balanced out the
11 facilitative effects in the grazed habitat of Nara Park for most of the growing season.

12 We hypothesize that the minimal effects of facilitation by *Urtica* are an evolutionary
13 consequence of a long history of grazing that selected for palatable genotypes or species with
14 small and prostrate growth forms. Plants with small phenotypes can survive alone in grazed
15 habitats by reducing grazer access, but they are competitively inferior. Therefore, small plants
16 may have experience competition rather than facilitation from large unpalatable species.
17 Facilitative effects in grazed communities are often observed in systems with short grazing
18 histories of a few years to a century (Oesterheld and Oyarzábal 2004). For example, Graff et al.
19 (2007) demonstrated positive effects of an unpalatable species, *Stipa speciosa*, on two palatable
20 grasses in a grass–shrub steppe community exposed to heavy sheep grazing since the end of
21 19th century. Bossuyt et al. (2005) reported clear evidence of facilitation effects in a 3-year
22 grazed grassland by domestic animals. In habitats with a short history of grazing, most
23 established plant species or genotypes have not evolved the abilities to tolerate, resist, and

1 avoid grazing and are thus very palatable. Therefore, unpalatable plants can greatly facilitate
2 the performance of grazing-sensitive neighboring plants.

3 In contrast, Rebollo et al. (2002) suggested that in grasslands with a long evolutionary
4 history of grazing, palatable species can independently tolerate or avoid grazing, rather than
5 using refuges of unpalatable species to avoid grazing pressure. To test this idea, one would have
6 to conduct a transplantation experiment that compares the balance of positive–negative
7 neighbor interactions between grazing-adapted small genotypes and grazing-sensitive large
8 genotypes of the target plant species.

9 Positive and negative effects of unpalatable plants on palatable neighbors potentially act
10 simultaneously, and the relative importance of the two effects depends on the difference
11 between the two species in vulnerability to grazing, which is determined by the defensive
12 ability of the unpalatable plants (Rebollo et al. 2005) and the resistance ability of palatable
13 species (Vandenberghe et al. 2009). Callaway et al. (2005) showed that two unpalatable
14 perennials, *Cirsium* and *Veratrum*, had strong positive effects on two palatable species, but had
15 no effect on another unpalatable species in a livestock grazed community. Baraza et al. (2006)
16 revealed that in high-grazed habitats, growth and survival of highly palatable tree saplings were
17 restricted to microhabitats under unpalatable shrubs with spines, whereas low-palatable
18 saplings could grow everywhere from bare soil to the understory of unpalatable shrubs. Our
19 results also suggest that the grazing vulnerability of species may influence the consequence of
20 their interactions, so that when both an unpalatable species and a palatable species are adapted
21 to grazed habitats in different ways, competitive rather than positive, interactions between them
22 may be increased.

23 This study found that *Urtica* individuals had slight positive effects on the growth and a

1 neutral effect on the survival and reproduction of *Persicaria*. The small phenotype of
2 *Persicaria* can survive alone in grazing habitats, even though it is grazed intensively by deer
3 (Suzuki 2008). This explains why the protective effects of *Urtica* only enhanced the growth of
4 *Persicaria* plants but not their survival. This study also demonstrated seasonal changes in the
5 negative and positive effects of *Urtica* on *Persicaria*. The seasonal variation in the effects of
6 *Urtica* may be attributable to seasonal variations in grazing intensity caused by changes in
7 herbivore behaviors and the irregular movement of herbivore populations (McNaughton 1984).
8 We have little information on seasonal variations in grazing pressure by deer in Nara Park, but
9 one report showed that the proportion of graminoids and herbs in the stomach contents of the
10 deer was largest during April–September (Torii et al. 2000). These periods correspond to the
11 periods during which positive effects of *Urtica* were observed in this study (for plant size in
12 May and for RGR in September–October). The lack of facilitative effects during the summer
13 season (June–August) may have been caused by changes in vegetation productivity (plant
14 biomass). In the periods when vegetation productivity is higher, grazing pressure is likely to
15 relatively decrease because of saturating food resources for deer, but competition intensity
16 among plants may increase because elevated plant biomass and plant height lead to severe
17 competition for light (Goldberg et al. 1999). Vegetation productivity is generally maximized
18 during the summer season within the study region. In a salt marsh community, Alberti et al.
19 (2008) also demonstrated that competitive interactions dominated in the spring and summer
20 when crab herbivory was low, whereas facilitative interactions dominated in the fall when
21 herbivory was highest. Together, these results suggest that the positive interactions are most
22 dominant during periods of the highest intensity of grazing, and support the current theory
23 predicting that interactions between plants shift from competitive to facilitative with increasing

1 grazing pressure (Graff et al. 2007). However, recent studies showed that facilitation effects are
2 strongest at intermediate grazing intensities (Brooker et al. 2006; Smit et al. 2007), and thus
3 conclusions on the relationship between plant interactions and environmental gradients are
4 open to debate.

5 In conclusion, although well-defended plants often facilitate other less-defended species,
6 we found that facilitative effects of well-defended *Urtica* on less-defended, but grazing-adapted
7 *Persicaria*, were limited in a plant community with a long history of intensive grazing. Our
8 findings suggest that diversification in grazing adaptation among plant species may alter the
9 intensity and direction of interspecific interactions in grazed communities.

10

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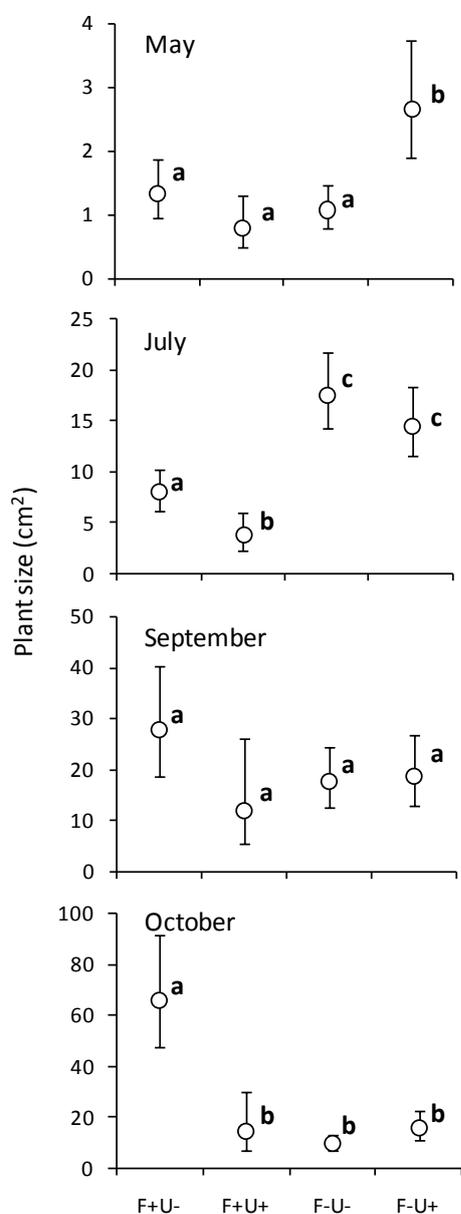
1 Table 1 Total number of *Persicaria longiseta* individuals and sizes of *Urtica thunbergiana* per
 2 plot. The values are shown separately for each treatment in four censuses.

	May	July	September	Oct
Total number of <i>Persicaria longiseta</i> individuals				
Fenced without <i>Urtica</i>	153	142	107	100
Fenced with <i>Urtica</i>	52	36	26	19
Unfenced without <i>Urtica</i>	272	207	129	79
Unfenced with <i>Urtica</i>	249	207	89	61
Size of <i>Urtica thunbergiana</i> per plot (cm ² , mean + SE)				
Fenced without <i>Urtica</i>	250 + 1.2	262 + 1.3	41.2 + 1.6	4.9 + 3.2
Fenced with <i>Urtica</i>	3315.9 + 0.7	3492.7 + 0.7	1611.6 + 0.8	2710 + 0.6
Unfenced without <i>Urtica</i>	464.4 + 1.7	382.4 + 1.4	146.8 + 1.2	90.8 + 1.5
Unfenced with <i>Urtica</i>	1353.6 + 0.5	2674.3 + 0.8	469.5 + 0.9	826.9 + 0.8

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1 **FIGURE LEGENDS**

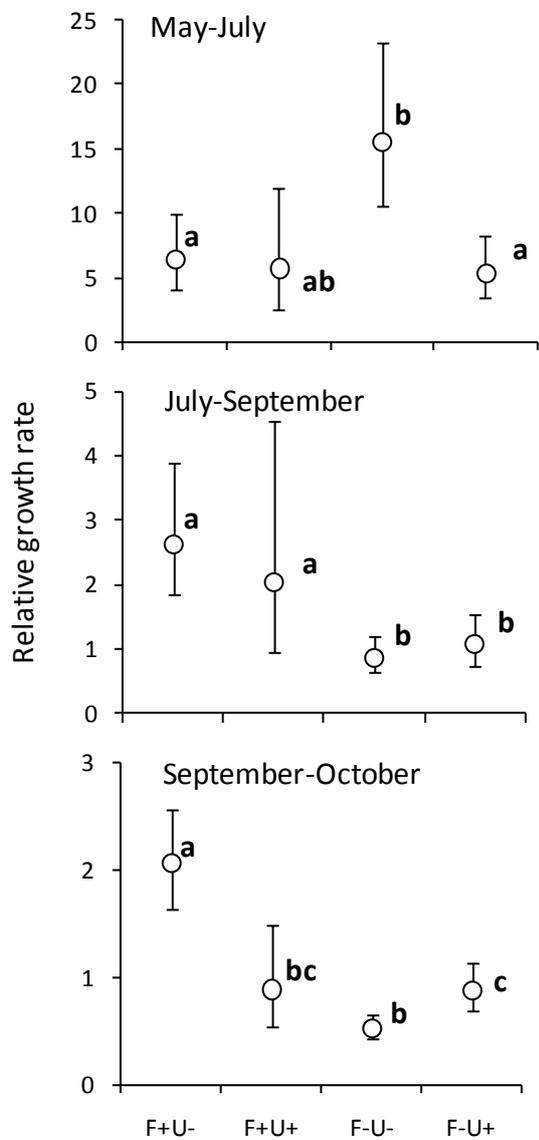
2 **Fig. 1** Effects of fences and presence of *Urtica* individuals on the plant size of *Persicaria* at
 3 four censuses. Treatments are shown by abbreviations: F+U-; fence with *Urtica* clipped,
 4 F+U+; fence with *Urtica*, F-U-; no fence with *Urtica* clipped, F-U+; no fence with *Urtica*.
 5 Points denote treatment means estimated from MCMC, and the intervals indicate least
 6 significant differences (different letters indicate significant differences among treatments at $P <$
 7 0.05).



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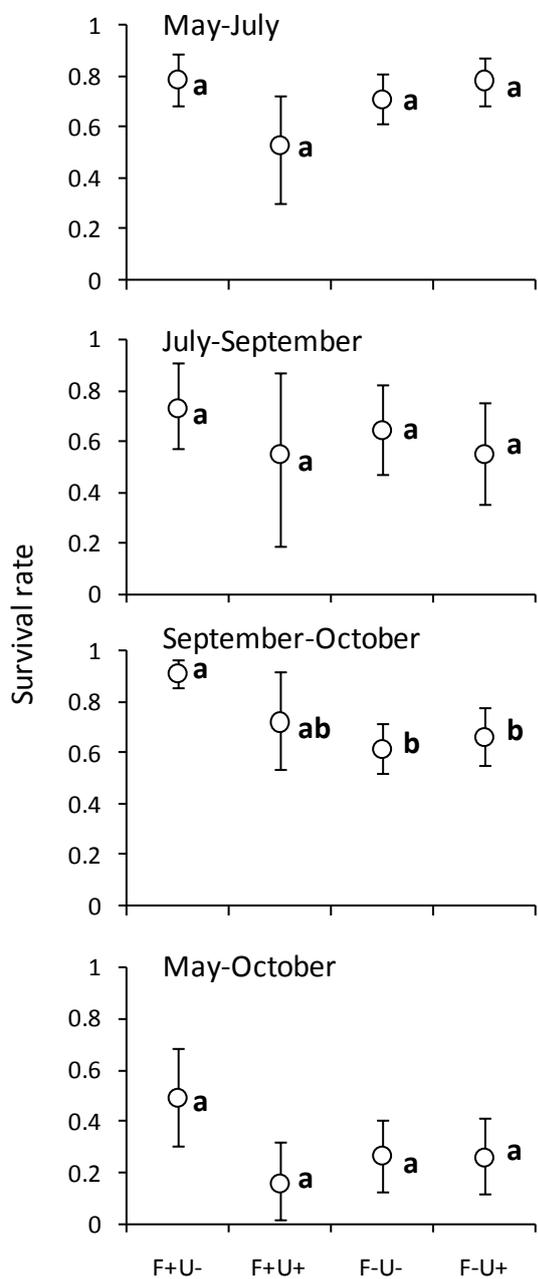
1 **Fig. 2** Effects of fences and presence of *Urtica* individuals on the relative growth rate of
 2 *Persicaria* during three periods. Results are shown as in Fig. 1.



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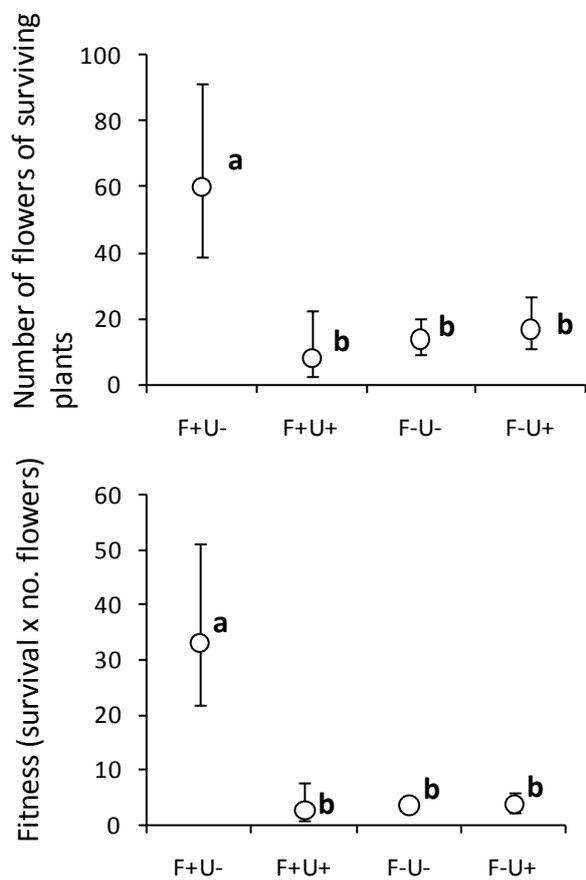
1 **Fig. 3** Effects of fences and presence of *Urtica* individuals on the survival rate of *Persicaria*
 2 during three periods. Results are shown as in Fig. 1.



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- 1 **Fig. 4** Effects of fences and presence of *Urtica* individuals on the reproduction of *Persicaria*.
- 2 Results are shown as in Fig. 1.



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