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3 **Distance-dependent shifts in net effects by an unpalatable nettle on a palatable plant**

4 **species**

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ABSTRACT

We examined whether the relative importance of facilitation and competition effects by an unpalatable perennial (*Urtica thunbergiana*) on a palatable annual (*Persicaria longiseta*) change with the spatial distance between them in a long-term deer-grazing habitat. Survivorship, growth, size, and fecundity of *Persicaria* were recorded at 1–2-month intervals during growing seasons in 2 successive years and were compared among individuals located in different positions relative to the canopy of *Urtica*: at the centre, internal edge, external edge, and far from the canopy. Survivorship of *Persicaria* was significantly higher at the centre of the *Urtica* canopy than outside the canopy early in the growing season in both years. No significant differences in *Persicaria* growth were observed among the four positions in most periods, except in one when growth was significantly higher at the centre, internal, and external edges of the canopy compared to outside the canopy. We found spatial shifts in the net effects of *Urtica* on *Persicaria* fecundity, from positive effects under the canopy centre to negative effects under the external edge of the canopy in the first year, and from negative effects under the centre to positive effects under the external edge in the second year. These results demonstrate that the relative importance of positive and negative effects of *Urtica* on *Persicaria* vary temporally within and among years and spatially around a single *Urtica* plant. Spatiotemporal variation in plant interactions may be attributable to annual and seasonal variation in vegetation productivity and grazing pressure.

Key words: competition, facilitation, deer-grazing, Nara Park, *Persicaria longiseta, Urtica thunbergiana*

1. Introduction

Plant–plant interactions, such as facilitation and competition, play a major role in shaping the structure of plant populations and communities (Callaway et al., 2005; Callaway et al., 2000; Callaway and Walker, 1997; Hacker and Gaines, 1997; Purves and Law, 2002). Facilitation and competition often act simultaneously (Callaway, 1994), and thus the net effect of a particular plant–plant interaction is determined by the relative strengths of the facilitative and competitive effects (Menge, 2000). The intensity of interactions among sessile plants gradually decreases with distance between individuals (Matlack and Harper, 1986; Weiner, 1984). How the interactions decrease with inter-plant distance and whether the intensities of facilitation and competition decrease similarly or differently depends on the species involved and the environmental context. Due to such contingency, it is less predictable whether the net effect of a plant–plant interaction changes with the distance between individuals.

Unpalatable plants with traits that deter animals, including toxicity, spines, and thorns, have potentially strong facilitative effects on palatable plants through indirect protection (Milchunas and Noy-Meir, 2002; Oesterheld and Oyarzábal, 2004; Osem et al., 2007; Rebollo et al., 2002; Smit et al., 2006). However, considerable evidence has demonstrated that such facilitation effects are balanced under some circumstances through competition between the palatable and unpalatable species (Alberti et al., 2008; Graff et al., 2007; Veblen, 2008). The balance between facilitation and competition depends on a variety of factors, e.g., grazing intensity (Graff et al., 2007; Levenbach, 2009), the defensive ability of the unpalatable plant (Rebollo et al., 2005), the grazing tolerance of the palatable species (Vandenberghe et al., 2009), community productivity (Goldberg et al., 1999; Rebollo et al., 2005), soil humidity (Veblen, 2008), and plant performance such as growth, survival, and reproduction (Maestre et al., 2005). Some studies

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1   have demonstrated that temporal variation in the effects of these factors can cause temporal

2   shifts in the balance between competition and facilitation (Alberti et al., 2008; Veblen, 2008).

3   However, few studies have examined spatial shifts in the net effects of unpalatable plants,

4   especially with respect to finer spatial scales around each unpalatable plant (but see Gómez et al.

5   2001).

6   We assumed that the strength of facilitative and competitive interactions and the net effect

7   of an unpalatable plant changes as a function of the distance between palatable and unpalatable

8   plants (Fig. 1). The net effect of an unpalatable plant on a palatable plant at each distance is

9   expressed as a combined function of facilitative and competitive effects. We hypothesised four

10 possible patterns for the net effect of an unpalatable plant changing with spatial distance. First,

11 when facilitative effects are greater than competitive effects, regardless of spatial distance, and

12 the two effects decrease similarly with distance, the net effect is generally positive and simply

13 decreases to zero over space (Case 1, Fig. 1a). The reverse case is also possible (Case 2, Fig.

14 2b). Most of previous studies have assumed that plant–plant interactions correspond to Case 1

15 or 2, but more complicated outcomes can occur when the strengths of competition and

16 facilitation change differently with spatial scale. For example, positive effects might be strong

17 below the canopy of the unpalatable plant and decrease abruptly from the centre to the edge,

18 whereas negative effects operate at an intermediate level below the canopy and decrease

19 gradually outside of the canopy (Case 3, Fig. 1c). In this case, the net effect is positive at the

20 centre of the canopy and negative near the edge of the canopy. This combination can arise when

21 competitive suppression that may be due to belowground competition operates at an

22 intermediate level at a wide range around the unpalatable canopy, whereas positive effects are

23 strong only at the centre of the unpalatable canopy because herbivores occasionally graze on

24 plants within the unpalatable canopy by inserting their heads through it. The opposite scenario

1 is also possible, that is, the net effect may be negative at the centre of the canopy and positive

2 near the edge of the canopy. This pattern can arise when competitive suppression through severe

3 shading is strong, whereas positive effects operate at an intermediate level at a wide range

4 around the unpalatable canopy because herbivores generally avoid grazing plants around

5 unpalatable plants but do occasionally (Case 4, Fig. 1d).

6   To test these hypotheses, we examined the spatial shift in net effects of unpalatable nettles

7 (*Urtica thunbergiana*) on palatable plants (*Persicaria longiseta*) at fine spatial scales around

8 unpalatable individuals in Nara Park, Japan, where a dense population of sika deer (*Cervus*

9 *nippon*) has persisted over a long time period. Our previous study demonstrated that *Urtica*

10 plants have protective effects on neighbouring *Persicaria* plants from deer grazing by

11 concealing them within the *Urtica* canopy (i.e., associational resistance), but they also have

12 negative effects on small neighbours, probably due to competition for light (Suzuki and Suzuki

13 2011). In this study, survivorship, growth, and fecundity of *Persicaria* specimens near *Urtica*

14 plants were recorded at 1–2-month intervals in 2 successive years. We classified *P. longiseta*

15 individuals into four distance classes based on the relative distance from the centre of the

16 nearest *Urtica* canopy, and compared performance among the distance classes. Our specific

17 question was whether the net effect on palatable plants shifted spatially from positive to

18 negative around an unpalatable plant (Case 3 or 4).

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21 **2. Materials and methods**

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23 *2.1. Study site*

24 The study was conducted at Nara Park (34°41' N, 135°50' E), in Nara Prefecture, western Japan

1 (see Suzuki and Suzuki, 2011 for details). Sika deer (*Cervus nippon* Temminck) populations

2 have been distributed in this park for more than 1200 years, as they are protected for religious

3 reasons. Over the last decade, the population density of deer has reached extremely high levels

4 (ca. 1200 individuals / 5 km^2 in the park; Foundation for the Protection of Deer in Nara Park,

5 2011). The study areas were established in a shady-moist environment in the understory of a

6 sparse Japanese cedar forest. Tall, erect species (e.g., *Erechtites hieracifolia* (L.) Raf., *Hypolepis*

7 *punctata* (Thunb.) Mett. ex Kuhn, and *Urtica thunbergiana*) were particularly abundant in this

8 environments (Suzuki et al., 2009). These tall species are unpalatable to deer because of their

9 physical and chemical defences (Kato *et al.* 2008).

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11 *2.2. Study species*

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13 We examined the interactions between a palatable species, *Persicaria longiseta* (De Bruyn)

14 Kitag., and an unpalatable species, *Urtica thunbergiana*. *Persicaria longiseta* is an annual herb

15 distributed widely throughout East Asia and is common to roadsides, farms, edges of rice fields,

16 and gardens in Japan. Seed germination occurs primarily from the end of March to April.

17 During the growing season, plants form a number of lateral shoots from axillary buds proximal

18 to the base. Flowering can start from July but occurs mostly from September onwards and

19 peaks in October at the study site. Reproductive plants produce a large number of small seeds

20 (*ca*. 1.5 mg per seed) but do not regenerate vegetatively. Fruit maturation and seed dispersal

21 occur from July to December. After reproduction, the plant dies by mid-December. Deer graze

22 individuals of *Persicaria* in Nara Park and the grazed plants exhibit inherently dwarf

23 morphology, with shorter shoots and smaller leaves compared with populations with no grazing

24 history (Suzuki, 2008). The small stature of *Persicaria* is likely a grazing response (Suzuki,

1   2008).

2   The nettle, *Urtica thunbergiana* is a perennial herb distributed within forest understories

3   throughout central and southern Japan. This species possesses stinging hairs containing toxins

4   on its stems and both surfaces of leaves, which can protect them from deer grazing (Kato et al.,

5   2008). During a growing season, plants develop a number of shoots proximal to the base. Most

6   aboveground parts wither during the winter season (December–March). The population of *U.*

7   *thunbergiana* in Nara Park has evolved an extremely higher density of stinging hairs compared

8   to those in ungrazed areas as a consequence of local adaptation to heavy grazing (Kato et al.,

9   2008). The maximum plant heights of *Persicaria* and *Urtica* in Nara Park are ca. 10 and 50 cm,

10   respectively, and thus *Urtica* plants seemingly suppress *Persicaria* neighbours through

11   competition for light.

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13   *2.3. Field censuses*

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15   In May 2007, we randomly selected 10 *Urtica* individuals and established ten 50×50-cm plots,

16   each positioned with an *Urtica* individual at the centre. Some plots included several *Urtica*

17   specimens. In June 2008, we established five 100×100 cm plots that contained several *Urtica*

18   individuals. We drove metal stakes into the ground at the corners of all plots. In total, 273 and

19   512 individuals of *Persicaria* and 17 and 18 individuals of *Urtica* were observed in 2007 and

20   2008, respectively (Table 1, 2).

21   All plants of the two species in each plot were mapped by recording the *x*,*y*-coordinates of

22   stems. Plant fates and sizes were recorded in May, July, September, and October 2007 (ten $50 \times$

23   50-cm plots), and in June, August, and October 2008 (five 100×100-cm plots). In October of

24   both years, the flowers on each *Persicaria* plant were also counted. To express plant size, we

1   measured the maximum diameter and the perpendicular diameter of the canopy (D_1 and D_2,

2   respectively) covered by the aboveground parts of each plant of the two species during each

3   census. As a measure of plant size, we calculated the area covered by each plant ($D_1 \times D_2 \times$

4     $\pi/4$).

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6   *2.4. Analysis*

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8   To standardize distances between palatable and unpalatable plants, we calculated a relative

9   distance between them by dividing the actual distance (from stem to stem) by the canopy size of

10   the unpalatable plant. The net effect of unpalatable plants on palatable plants was predicted to

11   vary nonlinearly with relative distance. One approach for modelling such a nonlinear

12   relationship is to fit a nonlinear function of the relative distance. However, models with

13   nonlinear functions might be too complex, making the interpretation of estimated parameter

14   values difficult. Therefore, we used a categorical variable for relative distance as an explanatory

15   variable. The positions of *Persicaria* plants were classified into four categories based on the

16   distance from the centre of the nearest *Urtica* canopy and the relative size of the *Urtica* canopy

17   as follows:

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19   - Centre of the canopy (position 1, P1): an area within one-half of the radius of the *Urtica*

20   canopy (relative distance < 0.5).

21   - Internal edge of the canopy (position 2, P2): an area under the canopy between the halfway

22   point of the canopy radius and the edge of the canopy ($0.5 < $ relative distance ≤ 1).

23   - External edge of the canopy (position 3, P3): an area from the limit of the radius of the *Urtica*

24   canopy to a distance 1.5 times the canopy radius ($1 \leq$ relative distance < 1.5).

1 - Far from the canopy (position 4, P4): an area beyond 1.5 times the canopy radius of the *Urtica*

2 plant ($1.5 \leq$ relative distance). The performance of *Persicaria* at P4 was regarded as a control

3 because we assumed that plants at P4 were rarely affected by *Urtica*.

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5 We also analysed *Urtica* effects using five position categories, including an outer position

6 (position 5: $2 \leq$ relative distance), but no significant differences were found between positions

7 4' ($1.5 \leq$ relative distance < 2) and 5, with the exception of two cases for which the general

8 trends were similar to the results of analysis with four positions. Therefore, we concluded that

9 *Urtica* rarely affected *Persicaria* individuals at P4.

10   By assuming that the shape of an *Urtica* canopy was a circle, the radius of the canopy was

11 calculated as [$\sqrt{\text{canopy size}/\pi}$]. The position category into which each plant was classified

12 varied between censuses because *Urtica* canopy size changed during the growing season. Thus,

13 the position categories of plants were determined during each census.

14   Survivorship and changes in plant size during periods between censuses, survivorship

15 during the whole growing season (May–October 2007 and June–October 2008), and final plant

16 size and fecundity (as the number of flowers) in October were analysed. For statistical analysis,

17 we used a generalised linear mixed model inferred by a Bayesian approach (Barker, 2010;

18 McCarthy, 2007). Bayesian inference is one of the most effective and robust methods to infer

19 parameters in a hierarchical model, especially when the number of replicates is limited or

20 unbalanced (Clark 2005; McCarthy 2007). The model formula is

21      $y_{ijk} \sim f(\mu_{ij})$

22      $g(\mu_{ij}) = \mu_0 + pos_i + plot_j,$

23 where y_{ijk} is the observed performance (i.e., survivorship, growth, plant size, or number of

24 flowers) of *Persicaria* individual k at position i in plot j, and it is assumed to follow an

1 appropriate distribution $f(.)$ [with a variance parameter if required], *binomial* for survivorship,

2 *normal* for growth, *Gamma* for plant size, and *Poisson* for the number of flowers; μ_{ij} is the

3 mean at position i in plot j; $g(.)$ is an appropriate link function, *logit* for survivorship,

4 *non-transformed* for growth, and *log* for plant size and number of flowers; $g^{-1}(\mu_0)$ [$g^{-1}(.)$ is the

5 inverse function of $g(.)$] is equal to a mean performance of *Persicaria* that are not affected by

6 unpalatable plants; a pos_i is an effect of position i as a fixed factor; and $plot_j$ is an effect of plot j

7 as a random factor following a normal distribution with mean of 0 and variance of σ^2_{plot}. In this

8 study, pos_4 (effect of position 4) was set to 0 by assuming no effects of *Urtica* at P4. Then,

9 position effects pos_i ($i = 1, 2, 3$) indicate the performance of *Persicaria* plants relative to those

10 at position 4, which could be equivalent to the relative neighbour effects (NUE, Markham, J. H.,

11 Chanway, 1996). A positive pos_i indicates that the net effect by *Urtica* is positive at position i.

12 Posterior means and credible intervals (Bayesian confidence intervals) of parameters were

13 estimated by Gibbs sampling, a Markov chain Monte Carlo method (MCMC). When the lower

14 limit of the credible interval of pos_i is higher than 0, the performance of *Persicaria* at position i

15 is significantly greater than that at position 4, which indicates that the net effect exerted by

16 *Urtica* on *Persicaria* at position i is positive.

17 Gibbs sampling was implemented using OpenBUGS 2.0 (Thomas, 2005) run through the

18 statistical package R v. 2.6.2 (R development Core Team, 2008) using the contributed package,

19 *R2WinBUGS* (Sturtz et al., 2005). Convergence of three independent chains was assessed via

20 the Gelman–Rubin statistic, and sufficient burn-in periods and thinning rates were used to

21 ensure satisfactory sampling of the posterior distributions.

22

23 **3. Results**

24 The observed values of the performance of *Persicaria* are shown in Table S1 in the Appendix.

1   In general, survivorship of *Persicaria* tended to be higher under the *Urtica* canopy than outside

2   of it (Fig. 2). In 2007, *Persicaria* survivorship in May–July was in the rank order P1 > P2 > P4

3   > P3 (Fig. 2a). The effect at P1 (centre of the *Urtica* canopy) was significantly positive. No

4   significant effects were found in July–September (Fig. 2b). Survivorship fell into the rank order

5   P1 > P3 > P2 > P4 in September–October, and effects at P1, P2 and P3 were significantly

6   positive (Fig. 2c).

7   In 2008, survivorship fell into the rank order P1 > P2 > P3 > P4 in June–August (Fig. 2d).

8   The effect on survivorship at P1 was significantly positive. No significant effects were found in

9   August–October (Fig. 2e).

10   Effects on *Persicaria* growth were not obvious during most periods. The growth of

11   *Persicaria* in May–July and July–September in 2007 did not differ among groups (Fig. 3a, b).

12   Growth was highest at P1 and lowest at P4 in September–October in 2007 (Table 1), and effects

13   at P1, P2, and P3 were significantly positive during this period (Fig. 3c). In 2008, growth tended

14   to be low at P1 and high at P3 in June–August and August–October, although these differences

15   were not significant (Fig. 3d, e).

16   Throughout the growing season (May–October), the effect on survivorship was significantly

17   positive at P1 in 2007 and 2008 (Fig. 4a, d). Final *Persicaria* plant size revealed a rank order of

18   P1 > P2 > P4 > P3 in 2007 (Fig. 4b), whereas a rank order of P4 > P2 > P3 > P1 was observed

19   in 2008 (Fig. 4e). The effects at P1 and P2 on plant size were significantly positive in 2007, but

20   no significant effect was observed in 2008.

21   A clear spatial shift in the effects on *Persicaria* fecundity was observed, although the

22   directions were quite different between the two years. In 2007, the effects on the number of

23   flowers produced per *Persicaria* individual were significantly positive at P1 and P2 and

24   significantly negative at P3 (Fig. 4c). In 2008, the effect at P1 was significantly negative, and

1   that at P3 was significantly positive (Fig. 4f).

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3   **4. Discussion**

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5   This study showed that the net effect of unpalatable *Urtica* plants was basically positive for the

6   growth and survivorship of palatable *Persicaria* individuals located under the *Urtica* canopy.

7   *Persicaria* survivorship throughout the growing season and final plant size were higher under

8   *Urtica* canopies than outside (Case 1, Fig. 1a). However, facilitative effects on survivorship

9   were not observed in several periods (July–Sept. 2007 and Aug.–Oct. 2008), nor were positive

10   effects found on growth over most periods, suggesting that the net effect of *Urtica* fluctuated

11   during the growing seasons. Moreover, we found spatial shifts in the effects of *Urtica* on

12   *Persicaria* fecundity, with the effect shifting from positive to negative (Case 3, Fig. 1c) or from

13   negative to positive (Case 4, Fig. 1d) at fine scales around the unpalatable plants. Based on

14   these results, we suggest that the relative intensity of competition and facilitation from *Urtica*

15   on the performance of *Persicaria* varies temporally within and among years and spatially at fine

16   scales around individual plants.

17   Our results suggest that *Urtica* had simultaneous competitive and facilitative effects on

18   *Persicaria*. Additionally, we recently conducted a field experiment that combined *Urtica*

19   removal and deer exclusion, and found that *Urtica* enhanced the growth of *Persicaria* outside

20   exclusion areas, whereas *Urtica* reduced *Persicaria* growth, survival, and reproduction inside

21   exclusion areas (Suzuki and Suzuki, 2011). These results confirm that *Urtica* suppressed

22   *Persicaria* competitively in addition to protecting it from deer grazing (associational

23   resistance).

24   The relative importance of facilitation is often highest during periods when grazing pressure

1   is heaviest, then decreases with grazing pressure (Graff et al., 2007). Seasonal variation in

2   grazing intensity may be caused by changes in herbivore behaviour and irregular movements of

3   herbivore populations (McNaughton, 1984). Seasonal variation in grazing intensity can also be

4   caused by changes in vegetation productivity (plant biomass) (McNaughton, 1985). Rich plant

5   biomass leads to lower grazing intensity because herbivores can obtain sufficient food material

6   within limited areas, but also leads to an increase in aboveground competition between

7   neighbour plants (Goldberg et al., 1999). The current study and our previous work (Suzuki and

8   Suzuki, 2011) show the lack of facilitation effects during the summer when plant biomass is

9   highest at the study site. Moreover, facilitative effects of *Urtica* were weaker during a year with

10   relatively higher productivity (i.e., 2008). Although the difference in *Urtica* effects between

11   years may have been attributable to the difference in plot size between years, because some

12   *Persicaria* individuals in position 4 could have been farther from *Urtica* specimens, our

13   generalised linear mixed model analysis that included an additional outer position (position 5)

14   indicated that the effects of *Urtica* were minimal outside the canopy. Therefore, the difference

15   in plot size had little effect on our results for positions outside the canopy (i.e., 1.5 < relative

16   distance < 2).

17   Our results demonstrate that the effects of facilitation and competition by *Urtica* plants on

18   neighbouring *Persicaria* operated at different spatial scales. Consequently, the balance of

19   positive and negative effects shifted between different distance categories around *Urtica* plants.

20   In 2007, *Urtica* effects on *Persicaria* fecundity were positive near the centre of the canopy but

21   negative at the external edge. A similar pattern was observed for final plant size, although it was

22   not significant. Hence, these results indicate that facilitative effects operated over a small range

23   near the canopy centre, but negative competitive effects operated over a longer range in the area

24   defined by the external edge of the canopy. The spatial shift in *Urtica* effects on *Persicaria*

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fecundity was also found in 2008, but the direction of the shift was reversed from that in 2007.

The shift from a negative effect at the centre of the canopy to a positive effect at the external

edge of the canopy suggests that competition exceeded facilitation under the canopy, whereas

facilitative effects operated at the external canopy edge where competitive effects became

relaxed. As suggested above, we predict that the reverse patterns might be caused by annual

variation in vegetation productivity, which is influenced by weather patterns. In 2007,

precipitation was lower than average in August (94 vs. 116 mm) and September (95 vs. 170

mm). The unusually dry conditions in late summer might have resulted in reduced plant growth

and increased grazing pressure during this season. Facilitative effects on fecundity in October

might have increased significantly under the canopy and declined drastically outside the canopy,

whereas weak competition for soil water operated over larger ranges. In contrast, the

precipitation pattern in 2008 (162 and 163 mm in August and September) was comparable to

that in an average year. Consequently, the weather conditions would have been suitable for plant

growth, and competitive interactions (especially aboveground) might have increased under the

unpalatable canopy, whereas weak facilitative effects might have operated over a spatial range

larger than the canopy radius.

Spatial shifts in net effects around a single plant have also been reported in other types of

ecosystems. In arid environments, shade effects (which inhibit soil evaporation) provided by a

shrub's canopy facilitate establishment, survivorship, and reproduction of other plants (Tirado

and Pugnaire, 2003). The spatial range of this kind of facilitation by a single plant is likely

smaller than the canopy radius (Barbier et al., 2008). In contrast, competition for water

resources in arid environments can operate over scales larger than the canopy radius because

shrubs have widely spreading root systems (Barbier et al., 2008; Meyer et al., 2008). In contrast,

van de Koppel et al. (2006) found that *Spartina alterniflora* provided large-scale facilitation and

small-scale competition on forb species on cobble beaches. This exertion of bidirectional effects

by individual plants may contribute to the spatially heterogeneous distributions and

performance of recipient species, heterogeneous community structure, and self-organised

patterns of vegetation structure (van de Koppel et al., 2006).

Although many studies have documented temporal and spatial variations in the balance

between facilitation and competition along gradients of environmental stress (Alberti et al.,

2008; Callaway, 1994, 1997; Graff et al., 2007; Menge, 2000; Oesterheld and Oyarzábal, 2004;

Russell and Fowler, 2004; Vandenberghe et al., 2009; Veblen, 2008), they have simply

concluded that the net effects of nurse plants are positive, negative, or neutral for recipient

plants within particular environmental conditions. In contrast, our study revealed that the net

effect of an unpalatable plant can vary spatially, even around a single nurse plant.

5. Conclusions

The balance between the positive and negative effects exerted by unpalatable plants on

palatable plants can shift both temporally and spatially at fine scales. We demonstrated the

complicated nature of plant–plant interactions, which contributes to the heterogeneous structure

of plant communities. As plants are sessile after germination, all interactions among them

inevitably depend on the distances separating individuals rather than the presence/absence of

neighbours. Therefore, to fully understand the ecological and evolutionary processes of plant

species, one must consider the spatial scales at which plant interactions operate.

6

7   **Appendix.** Supplementary data:

8   Table S1 Survivorship, growth, final plant size, and fecundity of *P. longiseta* plants in the four

9   positions.

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1   **Table 1**. Total number of *Urtica* individuals and mean radius of their canopy (standard

2   deviation between brackets) in each census.

	Number of plants	Radius of canopy (cm)
2007		
May	11	15.0 (4.6)
July	11	21.0 (7.4)
September	12	9.0 (4.1)
October	16	10.0 (5.0)
2008		
June	17	9.1 (5.5)
August	16	11.8 (6.6)
October	15	9.7 (7.1)

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1   **Table 2**. Total number of *Persicaria longiseta* individuals at each position *i* in each census.

	Position 1	Position 2	Position 3	Position 4
2007				
May	16	80	102	50
July	49	92	35	29
September	5	18	15	49
October	11	16	12	20
2008				
June	25	77	83	327
August	39	81	91	227
October	22	37	37	166

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Figure captions

Fig. 1 Possible shifts in the net balance between positive and negative effects at fine spatial scales. (a) Positive effects are greater than negative effects and the rates of decrease in influence with increasing distance from the unpalatable plant are similar; (b) negative effects are greater than positive effects and the rates of decrease with increasing distance from the unpalatable plant are similar between effects; (c) positive effects are greater than negative effects at the centre of the unpalatable plant canopy but decrease faster than the negative effects with increasing distance from the unpalatable plant; (d) negative effects are greater than positive effects at the centre of the unpalatable plant canopy but decrease faster than the positive effects with increasing distance from the unpalatable plant. Dashed, dotted, and solid lines indicate positive, negative, and cumulative (net) effects, respectively. The bold horizontal bar indicates the area covered by the canopy of an unpalatable plant.

Fig. 2 Effects of *Urtica* on *Persicaria* survivorship at position i, pos_i, in the periods May–July, July–September, and September–October 2007 (a–c), and June–August and August–October 2008 (d, e). Black circles are estimated means, thick vertical lines are 50% credible intervals, and error bars are 95% credible intervals. As position effects on the performance at P1-3 were estimated as differences from P4, the position effects for P4 (pos_4) that were set to 0 (white circles) are shown for comparison with the hypothetical patterns in Fig. 1 (same for following figures). The estimated performance at position i (see Table S1) is calculated as $g^{-1}(\mu_0 + pos_i)$ (see *Analysis*), and then μ_0 is equal to $g($[performance at the position 4]$)$.

Fig. 3 Effects of *Urtica* on *Persicaria* growth at position i, pos_i, in the periods May–July,

23

1   July–September and September–October 2007 (a–c), and June–August, and August –October

2   2008 (d, e).   Black circles are estimated means, thick vertical lines are 50% credible intervals,

3   and error bars are 95% credible intervals.

4

5   **Fig. 4**   Effects of *Urtica* on *Persicaria* at position i, pos_i, in terms of survivorship during whole

6   growing seasons (May–October) in 2007 and 2008 (a, d), final plant sizes (b, e), and number of

7   flowers per plant (c, f) in 2007 and 2008. Black circles are estimated means, thick vertical lines

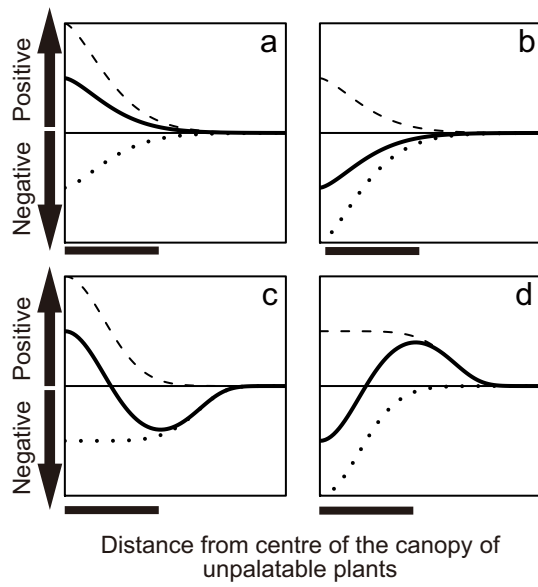8   are 50% credible intervals, and error bars are 95% credible intervals.

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Distance from centre of the canopy of
unpalatable plants

Fig.1

Fig.2

2007

(a) May-July

(b) July-Sept.

(c) Sept.-Oct.

2008

(d) June-Aug.

(e) Aug.-Oct.
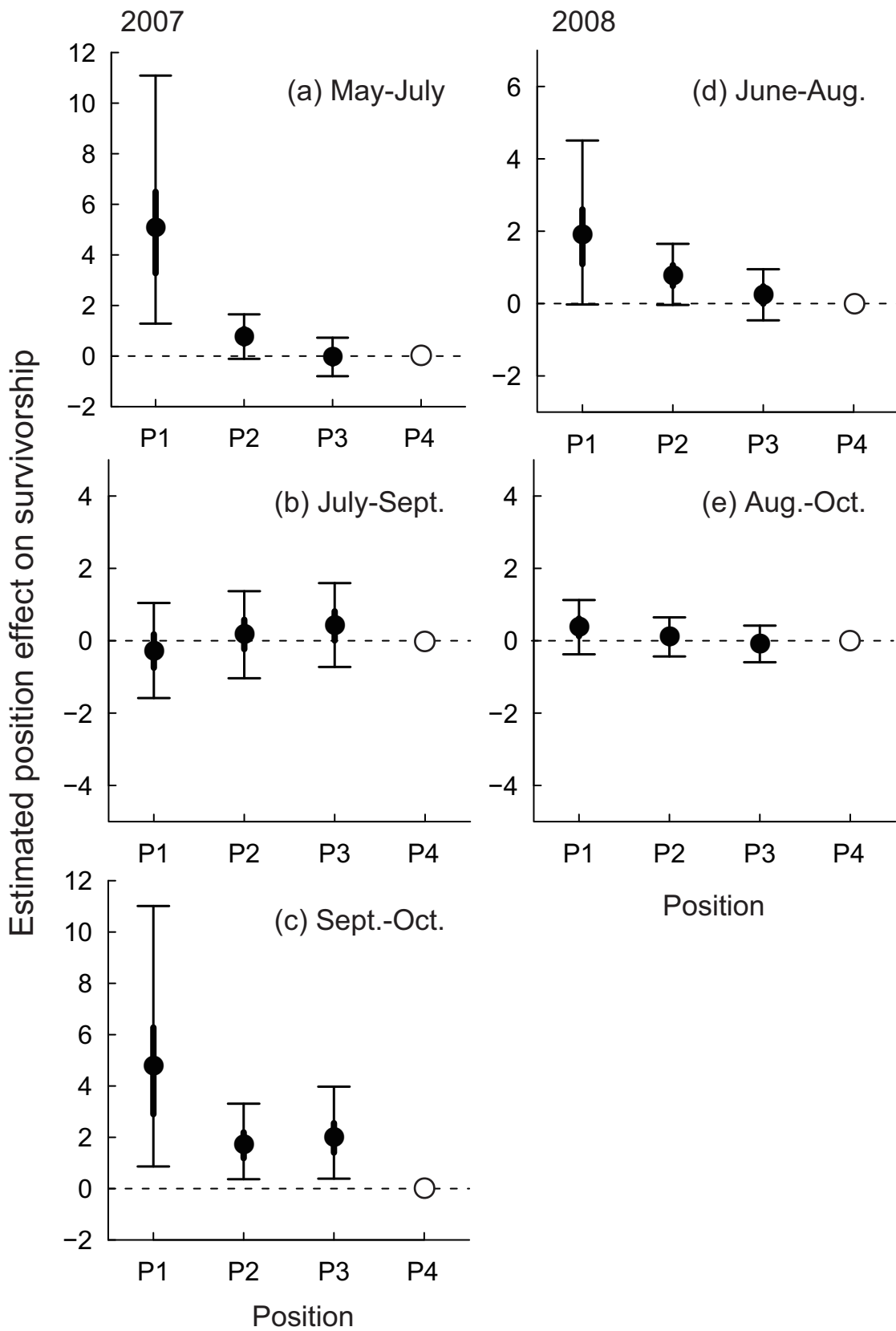
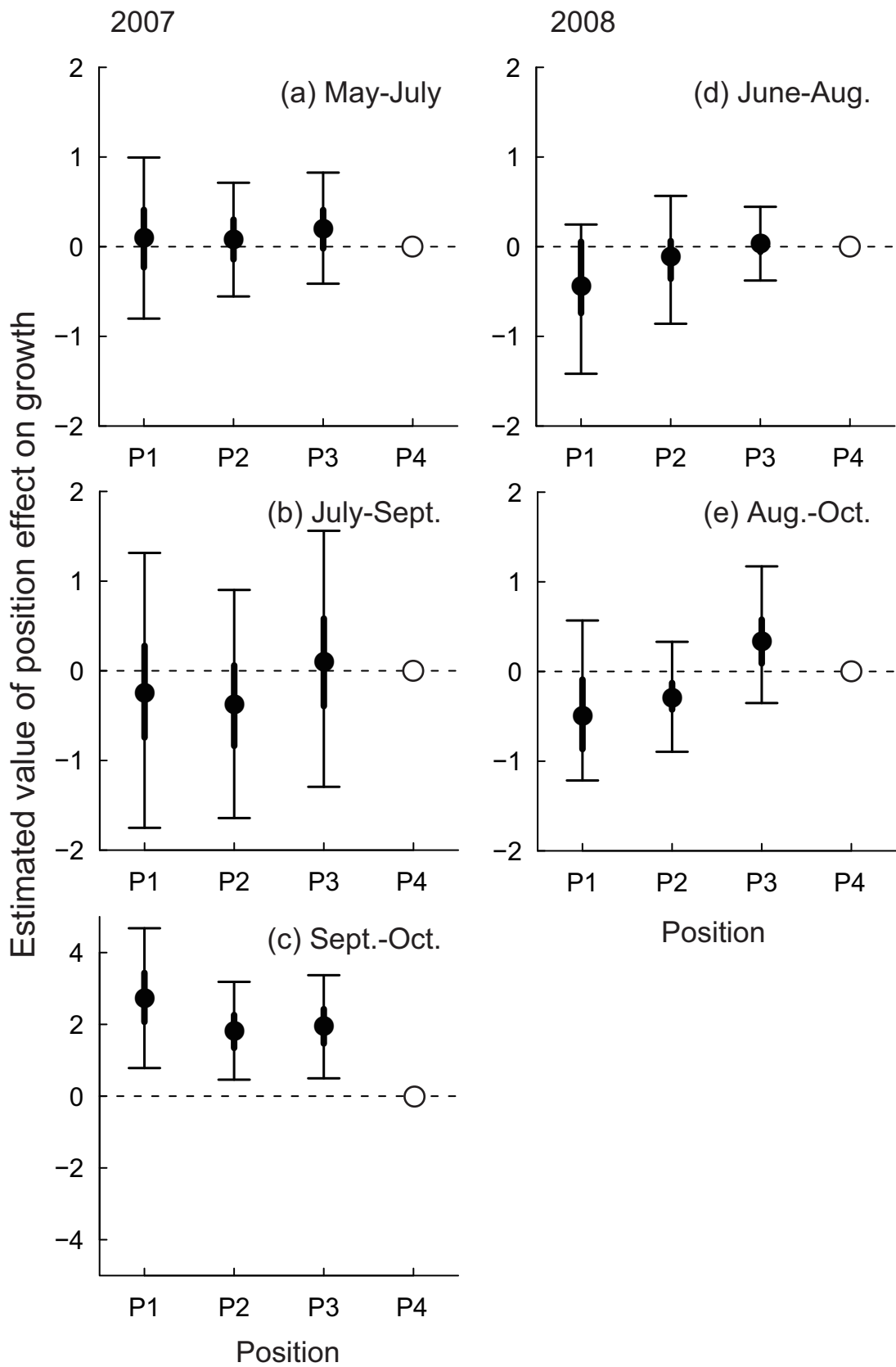Estimated value of position effect on growth
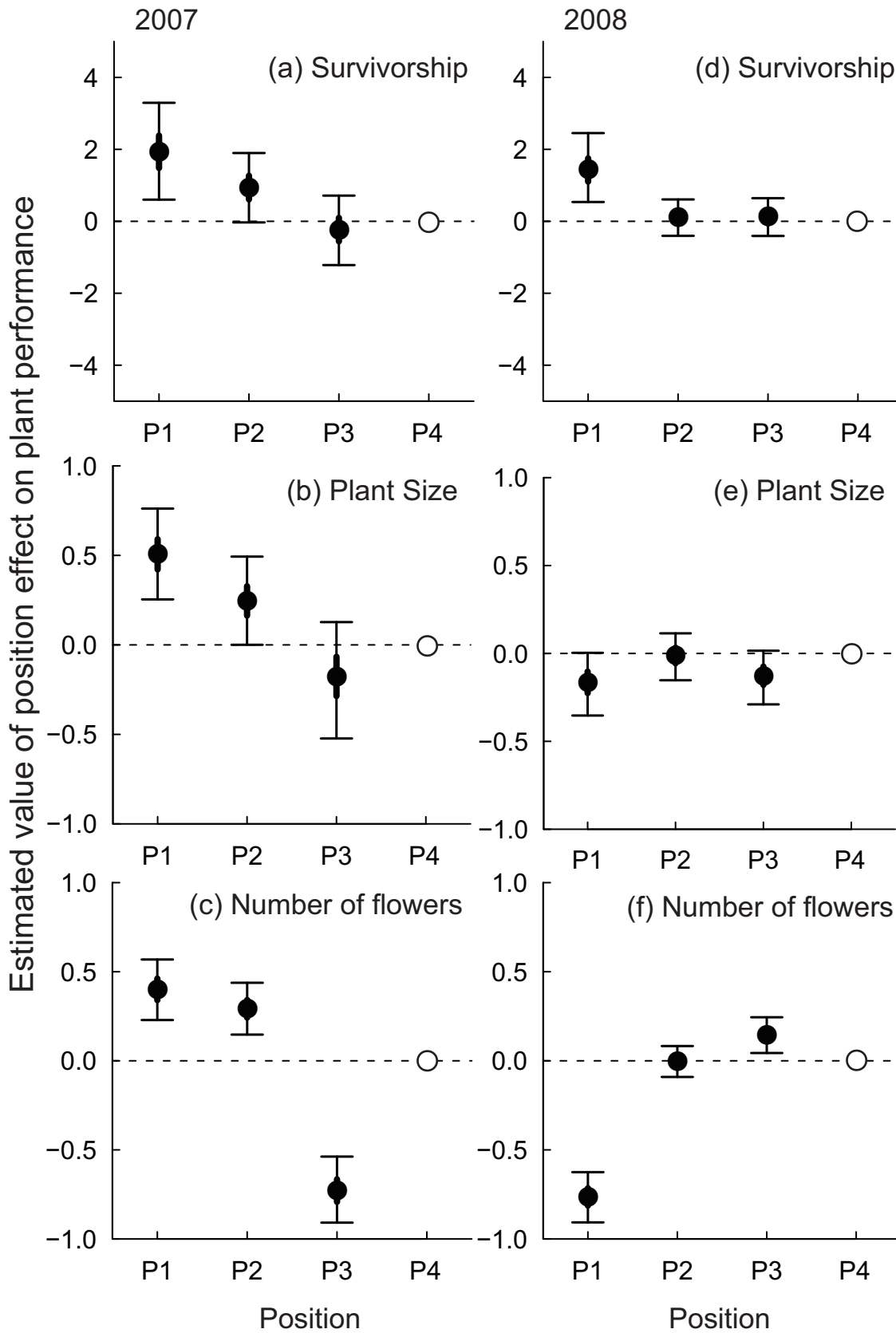
Position

Fig.3

Fig.4

1 **Appendix** Survivorship, growth, final plant size, and fecundity of *P. longiseta* plants in four positions relative to the *Urtica* canopy.   Posterior
2 mean, and lower and upper 95% credible intervals (between brackets) estimated by MCMC are shown.   Bold values indicate significant
3 differences from position 4 (i.e., the position effect deviated significantly from zero in Fig. 2-4).

	P1	P2	P3	P4
Survivorship				
2007				
May-July	**1.00 (0.91, 1.00)**	0.86 (0.71, 0.95)	0.74 (0.56, 0.90)	0.75 (0.52, 0.90)
July-Sep	0.43 (0.14, 0.78)	0.54 (0.24, 0.84)	0.60 (0.26, 0.88)	0.50 (0.16, 0.84)
Sep-Oct	**0.99 (0.71, 1.00)**	**0.85 (0.59, 0.97)**	**0.88 (0.62, 0.98)**	0.50 (0.33, 0.68)
May-Oct	**0.60 (0.22, 0.89)**	0.35 (0.11, 0.70)	0.15 (0.03, 0.42)	0.18 (0.05, 0.44)
2008				
June-Aug.	**0.98 (0.80, 1.00)**	0.93 (0.75, 0.99)	0.88 (0.65, 0.97)	0.85 (0.63, 0.96)
Aug.-Oct.	0.67 (0.48, 0.82)	0.61 (0.47, 0.76)	0.57 (0.42, 0.70)	0.58 (0.46, 0.70)
June-Oct.	**0.80 (0.61, 0.92)**	0.51 (0.37, 0.65)	0.51 (0.38, 0.65)	0.48 (0.39, 0.58)
Growth (cm^2)				
2007				
May-July	2.22 (0.97, 3.49)	2.20 (1.14, 3.28)	2.32 (1.30, 3.39)	2.12 (1.00, 3.26)
July-Sep	0.34 (-0.79, 1.46)	0.21 (-0.58, 0.99)	0.69 (-0.27, 1.70)	0.59 (-0.51, 1.61)
Sep-Oct	**1.29 (-0.48, 3.14)**	**0.37 (-0.66, 1.43)**	**0.50 (-0.65, 1.61)**	-1.45 (-2.29, -0.62)
2008				
June-Aug.	1.05 (0.15, 1.77)	1.38 (0.72, 1.97)	1.53 (1.18, 1.95)	1.49 (1.27, 1.74)
Aug.-Oct.	-0.28 (-0.97, 0.66)	-0.09 (-0.72, 0.43)	0.55 (-0.05, 1.27)	0.21 (-0.38, 0.60)
Final plant size (cm^2)				
2007	**6.07 (5.01, 7.25)**	**4.67 (3.81, 5.58)**	3.06 (2.26, 3.99)	3.66 (2.96, 4.42)
2008	5.27 (4.24, 6.56)	6.14 (5.17, 7.41)	5.47 (4.60, 6.73)	6.22 (5.47, 7.22)
Fecundity (No. of flowers per plant)				
2007	**20.10 (8.04, 44.48)**	**18.03 (7.25, 40.33)**	**6.51 (2.56, 14.47)**	13.46 (5.41, 30.04)
2008	**9.74 (4.22, 21.42)**	20.87 (9.18, 44.82)	**24.15 (10.52, 51.75)**	20.92 (9.13, 44.79)

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