

Floral trait expression and plant fitness in response to below- and aboveground plant–animal interactions

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Abstract

Although plant–animal interactions like pollination and herbivory are obviously interdependent, ecological investigations focus mainly on one kind of interaction ignoring the possible significance of the others. Plants with flowers offer an extraordinary possibility to study such mutualistic and antagonistic interactions since it is possible to measure changes in floral traits and fitness components in response to different organisms or combinations of them. In a three factorial common garden experiment we investigated single and combined effects of root herbivores, leaf herbivores and decomposers on flowering traits and plant fitness of *Sinapis arvensis*. Leaf herbivory negatively affected flowering traits indicating that it could significantly affect plant attractiveness to pollinators. Decomposers increased total plant biomass and seed mass indicating that plants use the nutrients liberated by decomposers to increase seed production. We suggest that *S. arvensis* faced no strong selection pressure from pollen limitation, for two reasons. First, reduced nutrient availability through leaf herbivory affected primarily floral traits that could be important for pollinator attraction. Second, improved nutrient supply through decomposer activity was invested in seed production and not in floral traits. This study indicates the importance of considering multiple plant–animal interactions simultaneously to understand selection pressures underlying plant traits and fitness.

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Introduction

In animal-pollinated plants, fitness is influenced by floral traits that function as an advertisement and reward for pollinators. In order to attain outcrossing, plants with flowers offer an extraordinary range of attractants to increase pollinator visitation. Floral advertisement includes olfactory cues, short-range tactile cues and visual cues, such as size, shape and colour

of inflorescences and flowers. Floral rewards include nectar and pollen that are highly sought by flower visitors (Dafni, 1992; Pellmyr, 2002). Floral advertisement and seed set can be affected by a range of organisms interacting with the plant. Investigations on the effect of leaf and floral herbivory documented that pollinator visitation is reduced in damaged plants through changes in floral traits (Lehtilä and Strauss, 1997, 1999; Strauss, 1997; Mothershead and Marquis, 2000). However, plant attraction to pollinators may also be affected by plant–animal interactions belowground. For example, *Sinapis arvensis* plants attacked by root

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herbivores had an increased flower visitation (Poveda et al., 2003). It is increasingly recognized that belowground and aboveground communities are highly interdependent (Gange and Brown, 1989; Moran and Whitham, 1990; Masters and Brown, 1992; Masters et al., 1993; Scheu and Parkinson, 1994; Nötzold et al., 1998; Bonkowski et al., 2001; Masters et al., 2001; Poveda et al., 2003). Understanding community and ecosystem level processes needs more information on the interactions between both subsystems. Studies on how belowground organisms affect flowering traits and seed set may lead to a more integrative view of the functioning of terrestrial ecosystems.

Belowground plant parts are attacked by root herbivores, and thereby, plant organs for nutrient and water uptake are damaged. Root herbivory is known to reduce flowerbud size and to delay the flowering period (Masters et al., 2001) but also to increase flower visitation rates (Poveda et al., 2003).

A second important belowground process is decomposition of organic material. The effects of decomposers on flowering traits have not been studied yet. Since decomposers are responsible for the breakdown of organic matter and the release and cycling of nutrients (Haimi and Einbork, 1992; Wardle, 2002), plants likely benefit from decomposer activity by the production of more attractive flowers for pollination, i.e. more and bigger flowers where nectar and pollen production is increased. Since in self-incompatible plants enhanced visitation of flowers by pollinators leads to an enhanced seed production, analyzing the mechanisms how decomposition and root herbivory influence floral traits and seed set is an important step in understanding below- and aboveground plant–insect interactions.

Important floral characters that have been shown to affect pollinator visits are the number of anthers (Krupnick et al., 1999), the amount and chemistry of nectar (Krupnick et al., 1999), the number and morphology of flowers (Karban and Strauss, 1993; Ohara and Higashi, 1994; Strauss et al., 1996; Lehtilä and Strauss, 1997, 1999), the flowering phenology (Strauss et al., 1996) and the height of the flowers (Strauss, 1997; Mothershead and Marquis, 2000; Hambäck, 2001).

This study was performed to investigate single and combined effects of main ecological processes such as decomposition, root- and leaf herbivory on plant growth, flowering phenology and on floral traits, as indicators of plant attractiveness to pollinators. However, it was not our objective to measure these effects on flower visitors, since we already did it in a previous experiment (Poveda et al., 2003). Additionally, we analyzed the effects of these three functional groups of plant-associated animals on seed production using *Sinapis arvensis*, a self-incompatible annual crucifer (Kunin, 1993). We expected negative effects of leaf

herbivores and positive effects of decomposers on floral traits and seed production. Although root herbivory may negatively affect floral traits (see above), our previous experiments showed that *Sinapis arvensis* L. (Brassicaceae) plants attacked by wireworms had an enhanced flower visitation (Poveda et al., 2003). Given these results, we expect positive effects of root herbivory on flowering traits which would mediate between the plant and the flower visitors. We also expect that below- and aboveground herbivores in combination more strongly affect floral traits and seed set. Furthermore, we expect that potential detrimental effects of herbivores on plant performance are counteracted by decomposers.

Materials and methods

Experimental set-up

The experiment was carried out under a gauze tent in an old fallow field close to Göttingen (Lower Saxony, Germany) in 2002. Two-liter pots were filled with defaunated soil, taken from a 10-year old fallow located on a limestone plateau east of Göttingen. The soil was defaunated by freezing at -20°C for 3 days. The pots were lined with a gauze-bag (1 mm mesh size) in order to prevent the escape of soil organisms from the pots and colonization by soil macrofauna from outside the pots. The bottom of each pot was filled with 200 ml gravel to facilitate drainage; 5 g litter material consisting mainly of grass leaves were placed on top of the soil. The litter was collected on a field margin, dried at 60°C and cut into pieces of about 2 cm in length. The experiment was set up in a three-way factorial design. The effects of root herbivores (R), decomposers (D) and leaf herbivores (L) on floral traits and components of plant fitness of mustard (*Sinapis arvensis*) were investigated. The full complement of possible combinations was set up (Control, D, R, DR, L, DL, LR, DLR) with six replicates each ($n = 48$ plants). Two earthworms of the species *Octolasion tyrtaeum* were added to each pot of the decomposer treatment. The density chosen (50 earthworms m^{-2}) is in the lower range of densities in the field (9–239 ind. m^{-2} ; Pizl, 1999). Earthworms were weighed prior to placement in the pots (average fresh mass of the two individuals 6.19 ± 0.7 g). Five wireworms (larvae of the click beetle *Agriotes* sp.) were added to each pot of the root herbivore treatments, which is equivalent to a density of ca. 125 individuals m^{-2} (average fresh mass 0.4 ± 0.03 g). Wireworms are patchily distributed in soil and may reach densities of up to several hundred per squaremeter (Poveda et al., 2003).

Seeds of *S. arvensis* from a regional wild population (provided by the Botanical Garden, Göttingen) were sown in the greenhouse on 29 April 2002. On 20 May

young seedlings that had 4–6 leaves were transplanted into the experimental pots, to which the soil organisms had been added 5 days before. One day after transplanting two third instar larvae of *Spodoptera litoralis* (obtained from Syngenta Crop Protection Mönchwilten AG, Stein, Switzerland) were put on the seedlings. The larvae were left on the plants until they had consumed ca. 50% of the leaves, which took approximately 2 days. All other subsequently produced leaves were left undamaged, to obtain an equal and reproducible amount of herbivory per individual. On 28 May all pots were set randomly in the tent. The gauze-tent (mesh size 0.1 mm) was constructed in order to prevent other insects from attacking the plants, while approximately maintaining ambient conditions of light, temperature and precipitation. The pots were buried into the soil to simulate natural temperature and moisture conditions for root herbivores and decomposers. During the flowering period plants were hand-pollinated using a mixture of pollen from other plants in order to secure cross-pollination between plants. Each day all open flowers were pollinated once, using a tooth-pick to deposit the pollen on the stigma. Rain was let to water all the pots naturally and during dryer weeks pots were watered with tap water.

Sampling and statistical analyses

For each plant the beginning and the end of the flowering period was noted. When plants began to flower the number of aborted flowers (the flower buds that never opened) was counted. Nectar production, anther length and size of the petals were measured for ten flowers of each plant. Nectar production and petal size was measured in the first opened flower (flower number 1) on the central stalk and then on all flowers with an uneven number, to flower 19. Anther length was measured on the second flower and on all even numbered flowers to number 20. We could not measure the same variables on the same flowers since anther size was measured in flowers that were about to open and petals had to be removed to reach anthers. Nectar production and petal size were measured the day after flower opening. In order to have a standardized estimate of nectar production, each morning from 7:00 to 8:00 all the liquid contained in the flowers was taken out with help of disposable capillary pipettes. After 1 h the quantity of nectar produced was extracted with a new capillary pipette for a volume of 1 μ l and the height of the nectar column was measured with help of a caliper. For each flower we measured the lengths and widths of the outer, showy parts (the limb) of the petals. Afterwards the area of each limb was calculated, as if it was an oval (length \times width $\times \pi$) and the sum of all four limbs would give the complete petal area. Anther length

was measured as an estimate of pollen production (method proposed by Kearns and Inouye, 1993). When flowers were about to open we measured the length of three out of the six anthers with help of a caliper. Since *S. arvensis* has four anthers on a long filament and two on a short one, we measured two anthers on a long filament and one anther on a short one. There was no difference in the length of the anthers on long filaments and on short filaments (*t*-test for matched pairs; $t = -1.17$, $P = 0.24$, $df = 479$). At the end of the experiment, when fruits turned yellow and the plant began to die (mid of July) plant height was measured. Also, fruits, roots and shoots were collected and dried for 3 days at 60 °C to determine dry mass. The number of fruits (= pods) of each plant was counted. Twenty fruits were randomly selected, and seeds per fruit were counted and weighed. These data were used to calculate the number of seeds and seed mass per plant. While washing the roots, earthworms and wireworms were collected and counted. At the end of the experiment 86% of the earthworms and 87% of the wireworms were present.

Data on plant biomass, number of flowers, flowering period and petal area were log transformed prior to statistical analysis to adjust to normal distribution and to increase homogeneity of variance. The data were analyzed using a multivariate analysis of variance (MANOVA). Protected ANOVA's were performed to locate which of the dependent variables responded most to the factors studied (Scheiner and Gurevitch, 2001). This procedure was preferred to Bonferroni corrections to avoid increased probability of type I error (Legendre and Legendre, 1998; Moran, 2003). There were significantly more differences than expected by chance (Moran, 2003; Table 1: the probability that eight out of 63 possible tests are significant by chance is 0.009 according to Bernoulli equation).

Differences between means were inspected using Tukey's honestly significant difference test. Correlations between the number of aborted flowers, flowering onset and the length of the flowering period were analyzed with Spearman's rank correlations. Statistical analyses were performed using Statistica 5 (StatSoft, 1995).

Results

Leaf herbivory had a significant effect on the variables studied (MANOVA; $F_{8,33} = 8.87$, $P < 0.001$); the effect of decomposers was marginally significant (MANOVA; $F_{8,33} = 2.15$, $P = 0.058$), whereas neither root herbivores nor any of the interactions between the factors studied significantly affected plant traits (MANOVA; $P > 0.1$). Separate ANOVAs indicated that leaf herbivores shortened the flowering period (Fig. 1A) and the

Table 1. Single ANOVA table of F values of the effect of root herbivores (R), decomposers (D) and leaf herbivores (L) on plant biomass, number of flowers produced, length of the flowering period, anther length, petal area, amount of nectar produced, fruits produced per flower and seed biomass in each plant (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

	df	Biomass	Flowers	Flowering period	Anther length	Petal area	Nectar	Fruits/flower	Seed mass
R	1, 40	2.08	0.56	0.44	0.39	0.30	0.01	0.01	0.37
D	1, 40	6.08*	1.72	0.43	1.76	0.35	0.68	4.82*	5.57*
L	1, 40	2.02	0.001	7.31**	25.43***	31.07***	3.47	1.03	1.90
RD	1, 40	1.08	1.44	1.00	1.86	0.30	0.95	1.12	0.22
RL	1, 40	0.44	0.02	0.49	1.99	2.38	0.19	0.82	0.13
DL	1, 40	1.95	0.66	0.00	0.04	0.067	1.79	5.31*	1.20
RDL	1, 40	1.51	1.54	0.02	0.05	0.02	1.32	0.28	0.25

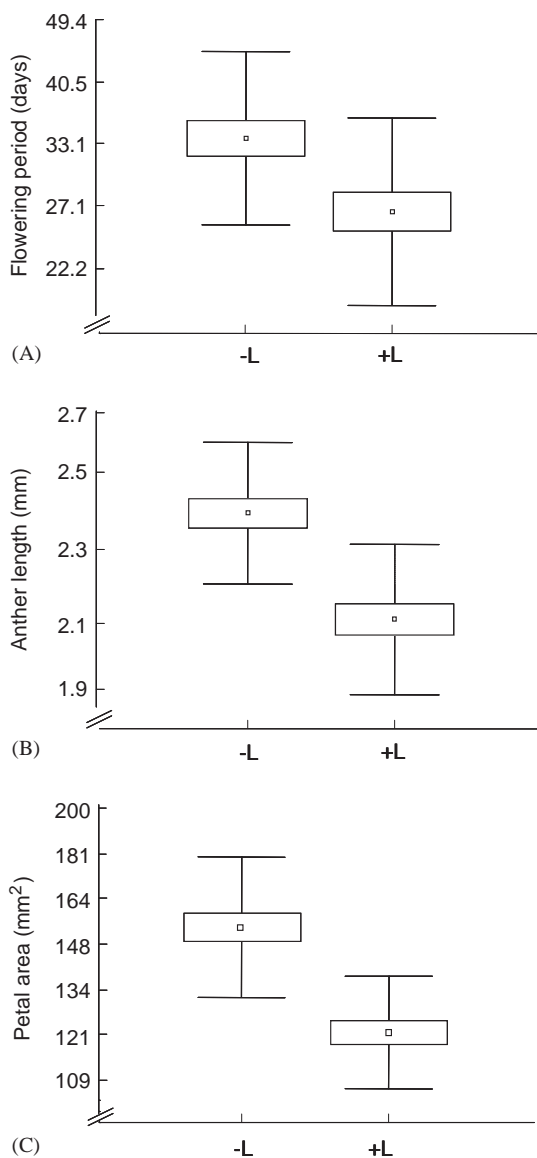


Fig. 1. Effects of leaf herbivores (L) on the flowering period, the length of the anthers and petal area of *Sinapis arvensis* (mean \pm 1SE and 1SD).

length of the anthers (Fig. 1B) and reduced the petal area (Fig. 1C, Table 1). A shorter flowering period was correlated with a higher number of aborted flowers at the beginning of the flowering period ($r = -0.43$, $P = 0.002$) and a delay in the flowering onset ($r = -0.37$, $P = 0.009$). There was no single or combined effect of root herbivores or decomposers on floral traits (Table 1). Decomposers increased total biomass (Fig. 2A), seed mass per plant (Fig. 2B) and the number of fruits per flower (Fig. 2C, Table 1). Seed mass per plant was correlated with the number of seeds ($r = 0.93$, $P < 0.001$). The number of fruits per flower was higher when decomposers were present but leaf herbivores were absent compared to when decomposers and leaf herbivores were absent (Fig. 2D, Table 1). Root herbivores and interactions between root herbivores and other factors did not affect plant growth, floral or seed production traits (Table 1). There was no effect of any treatment on the amount of nectar and the number of flowers produced by the plants (Table 1).

Discussion

Flowering characters, such as the length of the flowering period, petal area and anther length, were detrimentally affected by leaf herbivores, while root herbivory and decomposers did not affect flowering phenology and flowering characters. Other characters relating to plant growth and seed production, such as plant biomass, seed mass per plant and number of fruits per flower, benefited from decomposers but not by above- and belowground herbivores.

The importance of leaf herbivory in modifying floral traits and thereby attractiveness and rewards for flower visitors has been reported previously (Quesada et al., 1995; Strauss et al., 1996; Lehtilä and Strauss, 1997). Herbivores reduce leaf area and photosynthetic surface which relates to a lower rate of net photosynthesis (Crawley, 1997). Plants may compensate this loss

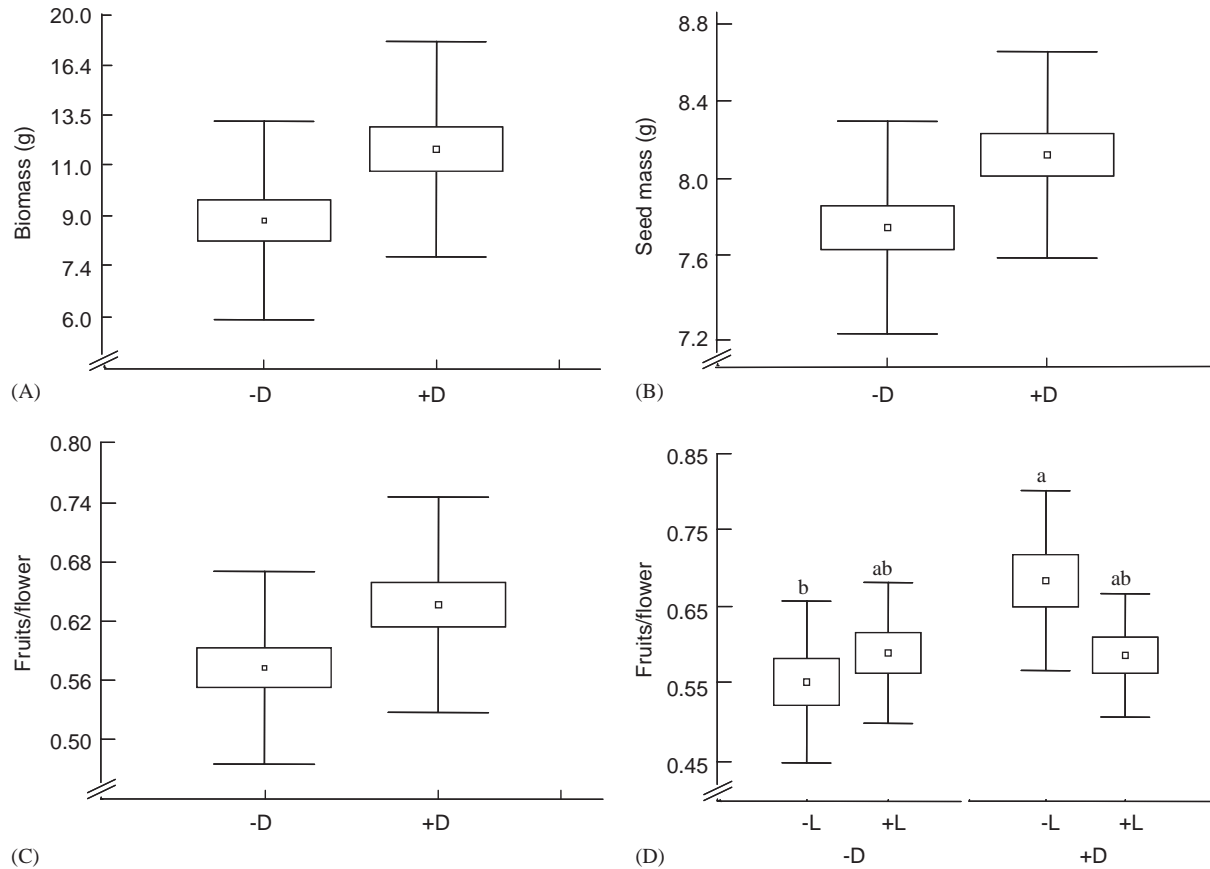


Fig. 2. Effects of decomposers (D) and leaf herbivores (L) on plants biomass, seed mass per plant, and the number of fruits per flower of *Sinapis arvensis* (mean \pm 1SE and 1SD). Treatments with different letters are significantly different (Tukey's test, $P < 0.05$).

through a variety of mechanisms. Crawley (1997) proposed that plants redistribute the photosynthate to the production of new leaves and away from roots, flowers, fruits or storage organs. By this, mustard may have compensated the damage caused by leaf herbivores by producing more leaves and aborting the first flowers, thereby delaying the onset of flowering and reducing petal size and pollen production. This would cause a reduction in flower attractiveness to pollinators, since it has been shown for other Brassicaceae, that plants with smaller flowers and a reduced amount of pollen are less visited than flowers with bigger petals and more pollen (Lehtilä and Strauss, 1997). It is surprising, however, that the effects of leaf herbivory on flowering characters remained unaffected by root herbivores and decomposers.

Root herbivory did not affect plant growth and seed production which is in contrast to previous studies (Brown and Gange, 1990; Masters et al., 2001). The results suggest that *S. arvensis* compensates for root damage. However, it has been reported that root herbivory may enhance flower visitation (Poveda et al., 2003), but this may have been caused by other cues than the ones measured in this study, e.g. changes in odour,

nectar concentration and flower colour (Dafni, 1992; Pellmyr, 2002).

Presence of decomposers (earthworms) enhanced plant and total seed biomass and fruit development per flower, but did not affect flowering traits. This suggests that *S. arvensis* does not invest extra nutrients for increasing floral attractiveness, but in increasing plant growth and seed development.

Seed production is determined by the number of flower buds, the rate of pollination, the rate of flower and fruit abortion, the number of seeds ripened per fruit, the amount of nutrients available and the rate of predispersal fruit predation (Stephenson, 1981; Crawley, 1983). Results of the present experiment document that plants in all treatments produced a similar number of flowers, and under optimal pollination (hand pollination) plants with decomposers produced more fruits per flower than did plants in treatments lacking decomposers. This suggests that decomposer-mediated increase in nutrient supply benefits plants when pollination is not a limiting factor. Increased nutrient mobilization by earthworms has been reported frequently (Scheu and Parkinson, 1994; Alpehi et al., 1996) and increased nutrient supply by decomposers was

probably responsible for the increase in plant and seed biomass in this study.

Female fecundity is limited by pollen delivered to the stigmas and resources for maturation of fruits and seeds (Haigh and Westoby, 1988; Larson and Barrett, 2000). If pollen limits seed set, selection favours increased allocation to pollinator attraction at the expense of ovule investment, but in species receiving excess pollen, a shift from attractive investment to ovules is favoured. The pattern found in *S. arvensis* suggests that this plant species faced no strong selection pressure from pollen limitation, since reduced nutrient availability through leaf herbivory affected primarily floral traits important for pollinator attraction. Further, improved nutrient supply through decomposer activity was invested in other plant fitness traits, such as number and size of seeds and reduced fruit and seed abortion.

In conclusion, leaf herbivory strongly affected flowering phenology and flower development, suggesting that leaf herbivory may alter the attractivity of plants for pollinators. In contrast, floral traits and seed production appear to be little affected by root herbivores. Decomposers enhanced plant biomass and fruit and seed set, but did not affect floral traits. This suggests that decomposers increase female fitness. It is challenging to investigate the evolutionary forces which resulted in the observed plasticity of responses of *S. arvensis* to the complex of plant-associated invertebrate guilds and relate these to other plant species of different functional groups and with different life histories. Ultimately, these studies may lead to a more detailed understanding of how belowground and aboveground plant–animal interactions shaped the evolution of plant traits.

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