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**THE SIGNALING FUNCTION OF AN  
EXTRA-FLORAL DISPLAY: WHAT SELECTS  
FOR SIGNAL DEVELOPMENT?**

by

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**Discussion Paper # 468**

**November 2007**

**מרכז לחקר הרציונליות**  
**CENTER FOR THE STUDY  
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# The signaling function of an extra-floral display: what selects for signal development?

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## ABSTRACT

The vertical inflorescences of the Mediterranean annual *Salvia viridis* carry many small, colorful flowers, and are frequently terminated by a conspicuous tuft of colorful leaves ("flags") that attracts insect pollinators. Insects may use the flags as indicators of the food reward in the inflorescences, as long-distance cues for locating and choosing flowering patches, or both. Clipping of flags from patches of inflorescences in the field significantly reduced the number of pollinators that arrived at the patches, but not the total number of inflorescences and flowers visited by them. The number of flowers visited per inflorescence significantly increased with inflorescence size, however. Inflorescence and flower visits rates significantly increased with patch size when flags were present, but not after flag removal. 6% of the plants in the study population did not develop any flag during blooming, yet suffered no reduction in seed set as compared to flag-bearing neighboring individuals. These results suggest that flags signal long-distance information to pollinators (perhaps indicating patch location or size), while flower-related cues may indicate inflorescence quality.

Plants that do not develop flags probably benefit from the flag signals displayed by their neighbors, without bearing the costs of flag production. Thus, flag-producing plants can be viewed as altruists that enhance their neighbors' fitness. Greenhouse-grown *S. viridis* plants allocated  $\leq 0.5\%$  of their biomass to flag production, and plants grown under water stress did not reduce their biomass allocation to flags as compared to irrigated controls. These findings suggest that the expenses of flag production are modest, perhaps reducing the cost of altruism. We discuss additional potential evolutionary mechanisms that may select for the maintenance of flag production.

## INTRODUCTION

The conspicuous visual displays of flowering plants attract pollinating insects, and promote plant reproductive success (Faegri & van der Pijl, 1979, Chittka & Thomson, 2001). Most of these displays are located in the corolla, and surround the reproductive organs of a single flower. In some cases, however, prominent visual signals are located at a distance from the flowers (extra-floral displays), while floral corollas are rather small and unremarkable (Heywood, 1978; Proctor et al., 1996). "Flags", large tufts of colorful bracts at the top of vertical inflorescences, provide a striking example of extra-floral displays.

Flags have long been claimed to attract insect pollinators, but the empirical support for this claim is scant and equivocal (Herrera, 1997, Arnon et al., 2006). Evidence for the pollination role of flags has been found in the Mediterranean annual *Salvia viridis* L. (Lamiaceae). In this species, experimental clipping of flags from inflorescences in a field population reduced insect visitation. Flag size in greenhouse-grown plants correlated positively with the number of open flowers per inflorescence, and with their nectar content (Arnon et al., 2006). A possible interpretation of these findings is that flags may function as signals of plant quality ("selective cues") to pollinators (Cohen & Shmida, 1993). Such signals may be very effective from the plant's point of view, because each flag advertises the quality of a whole inflorescence, rather than of a single flower (Faegri and van der Pijl, 1979; Gottsberger and Hartmann, 1988). We designate this possible selective advantage of flag displays as the "quality signaling" hypothesis.

A second possibility as to the adaptive function of flags is that they increase the long-distance visibility of *S. viridis* plants to pollinators (the "detection" hypothesis) (Herrera, 1997). That is, flags may function as "detective cues", or as

signals of patch size, rather than indicating the quality of individual plants. Plant quality may be signaled by other cues, such as plant height, number of flowers, flower size or additional visual cues associated with the flowers. Similarly, conspicuous unripe fruit within fruit clusters in *Pistacia terebinthus* increase the long-distance detectability of the whole cluster to seed dispersers (Fuentes, 1995). The "detection" hypothesis and the "quality signaling" hypothesis are not mutually exclusive, and flags may in fact signal both patch location and plant quality.

In this study we investigated the role of flags in plant quality signaling vs. long-distance advertising, using *S. viridis* as a model. This is a common spring-flowering annual in Mediterranean and Irano-Turanian grasslands. The protandrous flowers are arranged in whorls around the stem, and flowering progresses from the bottom of the inflorescences upwards. The upper lip of the corolla is dark purple while the lower lip is light purple or white (Feinbrun-Dothan, 1978). Flag-like bract clusters, composed of several colorful (purple, pink, or white) leaves, develop at the top of inflorescences in some of the individuals. The proportion of flag-bearing individuals varies among populations. The first flags usually develop on the main inflorescence. Secondary inflorescences that develop later sometimes carry flags as well. The plant grows in dense patches and is mainly pollinated by bees, though self pollination is possible. Each flower produces up to four seeds. The closed, dry seed pods remain on the plant for 2-7 months before dispersal (unpublished data).

We used three tests to evaluate our hypotheses. The first test consisted of comparing insect visits to patches of *S. viridis* in a natural field population, before and after clipping of their flags. The "quality signaling" hypothesis predicts that flag clipping will affect **within**-patch foraging, i.e. that pollinators will make fewer visits to clipped inflorescences after entering a patch. The "detection" hypothesis, in

contrast, predicts that pollinators will approach un-flagged patches less often than control patches. That is, that flag clipping would affect pollinator movement **between** patches. Effects on foraging **between and within** patches are expected if flags function both as quality signals and as detection cues.

For the second test, we compared female fitness (estimated by seed set) between plants that produced flags in the field population, and plants that did not develop flags throughout their blooming. Plants that did not produce flags were rather rare, and were interspersed within patches of flag-producing individuals. The “quality signaling” hypothesis predicts lower fitness to individuals that do not carry flags than to flag-producing individuals, for two reasons. First, flagless individuals are predicted to receive fewer pollinator visits. Second, they are expected to be in poor condition to begin with, and may therefore be resource-limited. The “detection” hypothesis predicts no fitness advantage to flag-carrying plants over flagless individuals within a patch.

The third test focused on estimating the costs of the flag displays to *S. viridis* plants. This approach is based on the following logic: according to the “quality signaling” hypothesis, each plant would receive more pollinator visits if it carried larger flags. Flag size in *S. viridis* is variable however, and correlates positively with plant size, suggesting that the flag signal provides honest information on plant quality. Such honest communication can be maintained if the flag signals are costly to produce and/or maintain (Zahavi & Zahavi, 1997). In particular, honest signaling can evolve if flag expression is condition-dependent, i.e. smaller in poor-condition plants than in good-condition plants (David et al., 2000). The “detection” hypothesis, on the other hand, predicts a group-level benefit to flag-producing patches, but no individual benefit to any plant within a patch from carrying a large flag. Thus, this hypothesis

does not assume selection for excessively large flag signals, and does not require costly signaling to maintain their reliability. Allometric growth may account for the positive correlation between flag size and plant size, but this relationship is not predicted to be condition-dependent under the "detection" hypothesis. We estimated the costs involved in flag production by determining the biomass allocated to flags, flowers and foliage in greenhouse-grown plants at different stages of flowering. We also tested whether these costs are condition-dependent by measuring biomass allocation to flags in water-stressed plants and unstressed controls.

## METHODS

### Field study

We conducted field observations in a large population of *S. viridis* in the Ellah valley in central Israel during March, 2007. We estimated the proportion of flag-bearing inflorescences in the population in a random sample of 372 inflorescences in full bloom. We recorded flag length and the number of flag leaves for a sample of randomly selected inflorescences, as an estimate of the population distribution of flag size.

### Manipulations of flags and flowers

We observed pollinator activity on intact inflorescences, and following removal of their flags during three days of observation. For each observation (n=11) we chose a distinct patch of blooming *S. viridis*, and recorded the combined number of primary and secondary inflorescences. We observed the patch for ten minutes for insect visits. We recorded the number of open flowers and visited flowers, flag length and the number of flag leaves for each inflorescence that received insect visits. We

noted whether the visitor was a honeybee, a small solitary bee (smaller than a honeybee), a large solitary bee (larger than a honeybee), a fly, a lepidopteran or a beetle. We also recorded how many inflorescences each individual visited before leaving the patch. Return visits to a previously visited inflorescence were scored as an additional visited inflorescence. At the end of the 10-minute period, we clipped all flags from the tops of the inflorescences in the patch. We then observed the patch for insect visits for ten additional minutes. We noted the number and type of visitors, and the number of inflorescences and flowers per inflorescence visited by each pollinator in the clipped inflorescences. As a control, we also performed the complementary manipulation: using the same protocol, we determined pollinator activity on intact inflorescences, and following removal of their flowers. Flags were not manipulated in this treatment (n=7 pairs of 10-minute observations).

#### Female fitness of flag-carrying and flagless plants

We marked 60 flag-carrying plants, and 60 plants that did not carry flags when in full bloom, which grew in patches that we did not manipulate. At the end of the blooming season, but before seed dispersal, we recovered the surviving plants. We counted the number of whorls, number of flowers per whorl, and number of seeds per flower for the two largest inflorescences of each plant. This was used as an estimate of female reproductive success of non-manipulated plants with and without flags in the field.

#### Greenhouse study

In the greenhouse, we characterized **biomass allocation** to flag production throughout blooming, and tested the effects of **water stress** on flag development.



Potted *S. viridis* plants for both purposes were grown in a commercial nursery from seeds collected at the Hebrew University's botanic garden. Shortly before blooming, they were transferred into a 6×8 m experimental greenhouse. The plants were exposed to ambient light-dark and temperature conditions, and were watered 180 ml/day through drip irrigation between March 5 and April 5, 2007. Irrigation volume was gradually increased to 550 ml/day during April, as the weather became drier and hotter. The study was terminated at the end of April, when flowering ended.

For the determination of **biomass allocation** to flag production, we harvested plants at the opening of their first flowers, a week, two weeks and three weeks later (peak blooming). We harvested 20 plants at each time point, and recorded the dry weight of above-ground vegetative tissue (stems and leaves), reproductive organs (flowers and buds), and flags for each of them. To characterize **flag development under water stress**, we grew plants under a standard irrigation regime or a restricted irrigation regime (n=40 for each treatment). The plants in the restricted irrigation regime received 70% of the water amount supplied to control plants, in 5 irrigations per week. To reduce mortality of young plants (and hence unintended selection for drought-resistant phenotypes), we started the restricted irrigation regime only when the flags started developing. Thus, the restricted irrigation treatment typically started a few days before opening of the first flowers, and continued until the end of blooming. The plants in both treatments received no irrigation after the end of flowering. At the end of blooming, we determined the number of flowers and flags per plant, and the dry mass of the flags, flowers and seeds, and above-ground vegetative tissue. Two control plants and one water-stress plant were lost to insect herbivory after the end of blooming. This reduced the final sample size to 77.

## Data analysis

In the field study, we treated observations of the same patch, before and after flag removal, as paired. Using one-tailed Wilcoxon matched-pairs signed-rank tests, we tested whether flag clipping reduced the number of insect visitors, the number of visited inflorescences and the number of visited flowers per 10-minute observation period. We employed linear regression to test for the effect of the total number of inflorescences per patch (patch size) on the number of visitors, visited inflorescences and visited flowers per observation period. We tested this effect separately for the patches prior to flag clipping, and after flag clipping. We used stepwise forward regression (inclusion criterion 0.05, exclusion criterion 0.1) to test the effects of flag length, number of leaves per flag, and the number of open flowers on the number of successive visits by each visitor on an inflorescence.

## RESULTS

### Field study

93.8% of 372 inflorescences that were sampled at full bloom carried a flag. Mean ( $\pm$ SD) flag length was  $12.4 \pm 3.8$  mm. The mean ( $\pm$ SD) number of leaves per flag was  $5.06 \pm 1.47$  ( $n=285$  inflorescences from the flag-clipping manipulation). Flag length and number of leaves were significantly correlated (Pearson's correlation coefficient=0.44,  $p<0.001$ ,  $n=285$  inflorescences). In accordance with previous observations (Arnon et al., 2006), the number of flag leaves was also significantly correlated with the number of open flowers in the inflorescence (correlation coefficient=0.17,  $p<0.001$ ,  $n=382$ ).

Honeybees were the most frequent visitors (76.48% of all visits), followed by large solitary bees (17.79%), small bees (3.16%), flies (1.58%) moths (0.59%) and

beetles (0.40%). The number of insects that visited *S. viridis* patches was significantly higher prior to flag clipping than after their removal (Table 1, Wilcoxon matched-pairs signed-rank test,  $n=8$ ,  $p=0.04$ ). Inflorescence and flower visit rates (number visited during a 10-minute observation period) were not significantly reduced after flag clipping (Wilcoxon matched-pairs signed-rank tests,  $n=9$ ,  $p=0.37$  for number of inflorescences,  $n=11$ ,  $p=0.45$  for number of flowers). Inflorescence and flower visit rates significantly increased with patch size when flags were present, but not after flag removal (Fig. 1; ANOVAs for flag-carrying inflorescences:  $F_{1, 10}=20.48$ ,  $p=0.001$  for number of visited inflorescences,  $F_{1, 10}=23.73$ ,  $p<0.001$  for number of visited flowers). The number of visiting insects per observation, on the other hand, was not significantly affected by patch size in flag-bearing inflorescences ( $F_{1, 10}=0.24$ ,  $p=0.63$ ) nor in clipped inflorescences.

Flag-bearing inflorescences that were visited by insects had a mean length of  $12.2\pm 2.4$  mm and  $4.9\pm 2.1$  leaves ( $n=260$ ). We tested whether insects preferentially visited inflorescences with large flags by comparing these values with the data set of flag sizes, which was recorded without observations of insect visits. Flags of inflorescences that received insect visits did not significantly differ in size from the population means (two-tailed t-tests:  $t_{543}=0.40$ ,  $p=0.69$  for flag length;  $t_{515}=1.23$ ,  $p=0.22$  for number of leaves). The number of open flowers, but not flag length or flag leaf number, significantly affected the number of flowers visited per inflorescence (stepwise regression,  $r^2=0.121$ ,  $p<0.001$ ). In the complementary experiment, which involved clipping of all flowers from inflorescences, no insects landed on *S. viridis* inflorescences after the manipulation. Approaches to the patches with no landing on plants were not recorded.

Flag-bearing plants, and plants that did not develop flags, did not significantly differ in the numbers of flower whorls, flowers per whorl, and seeds per flower at the end of the blooming season (Fig. 2). We recovered 49 of the flag-carrying and 11 of the flagless marked plants (the remaining plants were grazed by sheep), suggesting higher survival of flag-bearing plants.

### Greenhouse study

As flowering progressed, plant allocated increasingly more biomass to the production of flowers and seeds, while the fraction of biomass allocation to leaves and stems decreased. Allocation to flag production fluctuated, and accounted for 0.5% or less of the plants' total biomass (Fig. 3). Irrigation-restricted plants developed significantly fewer flowers, but not fewer flags, than control plants (no. flowers:  $118.56 \pm 46.26$  for irrigation-restricted,  $139.50 \pm 45.15$  for controls,  $t_{75}=2.01$ ,  $p=0.02$ ; no. flags:  $6.87 \pm 2.78$  for irrigation-restricted,  $7.42 \pm 3.07$  for controls,  $t_{75}=0.82$ ,  $p=0.21$ ). Water stress significantly reduced total plant mass, the biomass of vegetative tissue, and of flowers and seeds (Fig. 4 top,  $t_{75}=1.87$ ,  $p=0.03$  for total mass,  $t_{75}=1.92$ ,  $p=0.03$  for vegetative mass;  $t_{75}=1.68$ ,  $p=0.049$  for the mass of flowers and seeds). It did not, however, reduce the proportions of biomass allocated into vegetative, reproductive and flag tissue (Fig. 4 bottom,  $t_{75}=0.12$ ,  $p=0.45$  for vegetative tissue,  $t_{75}=0.20$ ,  $p=0.42$  for flowers and seeds;  $t_{75}=0.74$ ,  $p=0.23$  for the mass of flowers and seeds).

## DISCUSSION

Experimental flag clipping in patches of *S. viridis* in the field reduced the rate of insect arrivals into the patches, but not the rate of visits to inflorescences or flowers within patches. This implies that fewer individuals visited patches after flag removal,

but that each of them made a longer bout of visits before leaving the patch. The increased bout lengths may reflect the foragers' response to higher nectar and pollen yields in less-visited patches after flag clipping. Increased bout lengths in clipped patches may have also blurred the correlation between patch size and pollinator visit rates after flag removal (Fig. 1). Our experiment did not control for possible location learning by the foraging bees. That is, foragers may have relied on their previous experience and spatial memory, rather on the flag displays, to locate the clipped patches of *S. viridis*. Spatial memory is well-developed in bees, and can guide foraging choices (Wehner & Menzel, 1990), hence our observation procedure may have underestimated the effects of flag removal on the frequency of pollinator arrivals. Flag removal nevertheless significantly reduced pollinator arrivals, suggesting that the location effect was not dominant.

The results of the field manipulation are in line with the “detection” hypothesis, which proposes that flags increase the visibility of *S. viridis* patches to insects from large distances, while flower-related cues are used for making foraging choices within patches (Lewis, 1985, Armbruster et al., 2005). The following observations support the notion that flags are not the main cues for within-patch choice of inflorescences: (a) No insects landed on inflorescences after experimental removal of flowers, even though the flags were left intact; (b) The mean size of flags in inflorescences that were visited during observation sessions did not significantly differ from the population mean, suggesting no pollinator preference for inflorescences with large flags within patches. Additionally, the significant effect of the number of inflorescences on visit rates in flag-carrying patches suggests that patch size may affect within-patch bout length, as previously reported (e.g. Goulson et al., 1998, Grindeland et al., 2005).

Our findings resemble the results of flag-clipping manipulations in the perennial shrub *Lavandula stoechas* (Herrera, 1997): both studies provide evidence for increased insect attraction to flags at a large distance, but not when they forage within a patch. In addition, both studies did not demonstrate an increase in plant fitness due to the presence of flags. Our present results also generally agree with a previous flag manipulation study with *S. viridis* by our group (Arnon et al., 2006). Both studies demonstrate a significant decrease in the number of visitors following flag clipping. However, the Arnon et al. (2006) study also showed a marginally significant decrease in the number of inflorescences and flowers visited after flag removal, while no such trend was observed in the present study. The protocol of the earlier study differed from the present one in the following respects: a. flags were removed from whole patches (n=6), half-patches (n=3), or randomly from one half of the inflorescences within a patch (n=3). b. Manipulated patches were compared to nearby control patches of the same size, which were observed simultaneously. c. Observation periods were 30-180 minutes. We do not know which of the changes in observation protocols accounts for the differences in pollinator behavior between the two studies.

The two hypotheses that we tested make opposite predictions regarding the direction of selection that acts on flag display. The “quality signaling” hypothesis views flags as a secondary sexual trait. The theory of sexual selection is increasingly applied to the evolution of secondary displays in plants (e.g. Skogsmyr & Lankinen, 2002; Delph & Ashman, 2006). Sexual selection is predicted to favor exaggerated (super-stimulus) secondary displays, such as large flags, in all plants. Some sexual signals may reliably advertise their bearer's quality because they are costly, hence can only be produced and maintained by high-quality individuals (e.g. Kotiaho, 2002,

Cotton et al., 2004). In plants, costly signals were proposed to mediate honest communication with herbivores (Archetti & Brown, 2004) and competitors (Lev-Yadun, 2005). Applied to flags as quality indicators, this hypothesis predicts that flags are costly to produce and maintain, and that their expression depends on plant condition. The “detection” hypothesis views the production of flag as a trait that is expressed by some of the plants, but that benefits all the individuals in the patch through enhanced pollinator attraction. Individual selection should therefore favor “hitchhiker” individuals that do not carry flags, and grow in the proximity of flag-producing neighbors.

Our study shows that the costs of flag production, at least in terms of biomass, are quite modest. Water limitation reduced overall plant size, indicating that the treatment plants were stressed, but it did not reduce the relative biomass allocation into flag expression. Further, plants that did not produce flags in the field had similar female reproductive success as their flag-producing neighbors. These results are compatible with the “detection” hypothesis, and do not suggest that flags are condition-dependent costly handicap displays. It should be noted, however, that we did not measure other possible expenses of flag production, such as pigment production costs, or indices of male fitness.

If the benefits of the flag production trait are shared by hitchhikers that do not produce flags, how is this trait maintained in natural populations? One possible mechanism is kin selection: if individuals in a patch are genetically related, then flag-producing individuals may gain indirect fitness from the increased reproductive success of their neighbors. Such indirect benefits may select for an altruistic trait (such as flag production), if the associated costs to altruists are low enough (de Jong & Klinkhamer, 2005). Relatedness among individuals in a patch is expected in

synaptospermic taxa such as *Salvia*, which disperse their seeds in synchrony to a short distance (Zohary, 1950). The possibility of kin selection can be tested by assessing the relatedness of individuals within *S. viridis* patches, and by measuring the heritability of the flag production trait. Kin recognition, and traits that benefit genetic relatives, have been previously described in plants. One example involves restrained competition among roots of related individuals that grow next to each other (Dudley & File, 2007). A second proposed example involves the production of chemical signals by plants, to attract natural enemies of their herbivores. While most of these volatiles are produced by herbivore-infested plants, some are also produced by neighboring, non-infested plants. It has recently been suggested that this seemingly altruistic signal benefits the producers' relatives, and is maintained in the population through kin selection (Kobayashi & Yamamura, 2007).

Another possibility is that flag producers are not really altruists, because they increase their individual fitness through additional benefits, which are not related to female reproductive success. Protection from radiation and herbivory were suggested as possible survival advantages of extra-floral displays (Galen and Cuba, 2001; Armbruster, 2002). Our low recovery rate of marked, flagless plants at the end of the flowering season suggests that their survival may indeed be low as compared to flag producers. This possibility can be tested by a more rigorous and larger-scale comparison of the survival of plants with and without flags under field conditions.

Flag-like extra-floral displays are rather rare in plants; for example, they occur in only four genera in the Mediterranean flora (Arnon et al., 2006). They are also unique because of their clear spatial separation from the plant's reproductive organs, and their variable frequency across populations. We propose that these traits render



them valuable experimental models for studying the selective forces acting on reproductive plant signals.

#### ACKNOWLEDGEMENTS

Mimi Ron and Gali Meltzer (Meltzer Nurseries Ltd.) provided potted plants for experiments. Shalhevet Azriel, Ittai Malka, Naama Morag, Miriam Rosenberg, Frank Thuijman, Dean Foster, Scott Forbes and Tom de Jong participated in the field observations. Michal Segoli and Joel Sobel commented on the manuscript. The study was supported by the Center for Rationality and the Institute for Advanced Studies at the Hebrew University.

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Table 1 : Parameters of insect visits to *S. viridis* patches before and after flag removal.

Replicate no.	No inflorescences / patch	Before flag removal			After flag removal		
		No. inflorescences visited	No. flowers visited	No. visitors	No. inflorescences visited	No. flowers visited	No. visitors
1	64	8	13	4	8	18	1
2	60	22	32	5	8	9	1
3	60	20	25	3	29	49	1
4	76	18	26	6	9	12	4
5	80	8	15	3	1	2	1
6	8	12	19	1	32	72	1
7	150	31	43	4	30	52	4
8	200	39	60	2	24	35	4
9	40	4	1	6	4	5	4
10	50	11	13	3	12	15	3
11	30	13	16	5	18	21	6

## FIGURE LEGENDS

Fig. 1: The effect of patch size on the number of visited inflorescences (top), visited flowers (middle) and visiting insects (bottom). Full symbols denote intact patches, empty symbols denote patched after removal of all flags. Regression equations for intact and flag-removal patches are -

Top:  $y=0.161x+4.958$ ,  $r^2=0.69$  (intact);  $y=0.044x+12.614$ ,  $r^2=0.05$  (flag removal);

Middle:  $y=0.253x+5.095$ ,  $r^2=0.73$  (intact);  $y=0.036x+23.669$ ,  $r^2=0.01$  (flag removal);

Bottom:  $y=-0.005x+4.171$ ,  $r^2=0.03$  (intact);  $y=0.008x+2.149$ ,  $r^2=0.06$  (flag removal).

Fig. 2: Parameters of female reproductive success in plants that carried flags (black bars,  $n=49$ ) and flagless plants (white bars,  $n=11$ ) in the field. Error bars are 1 SD.

Fig. 3: Dry biomass of flags, flowers and buds, and vegetative tissue in greenhouse-grown plants. Plant samples ( $n=20$  per sample) were harvested at the beginning of blooming, and one, two and three weeks later. Error bars are 1 SD.

Fig. 4: Dry biomass (top), and proportions of biomass allocation to flags, flowers and buds, and vegetative tissue (bottom) in plants grown without irrigation restriction and under water stress in the greenhouse. Plants were harvested at the end of flowering. Error bars are 1 SD.

Fig. 1

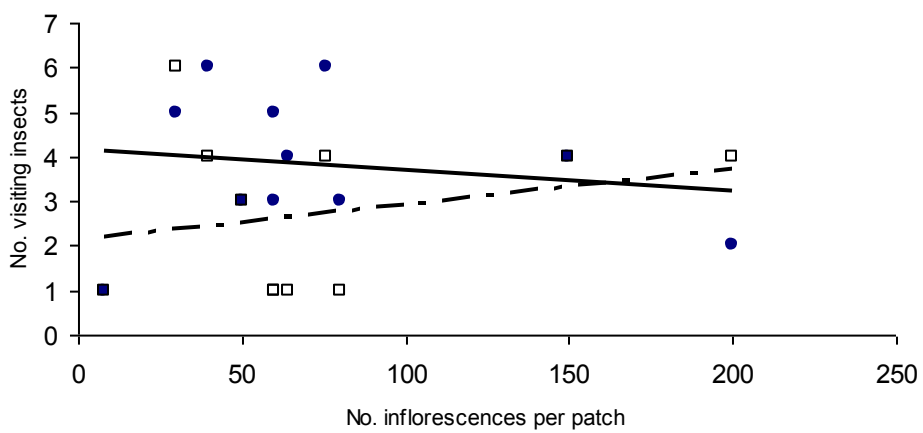
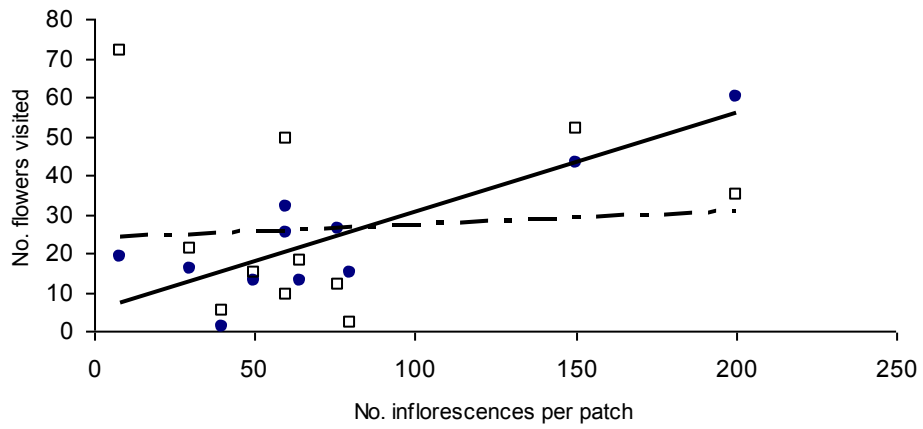
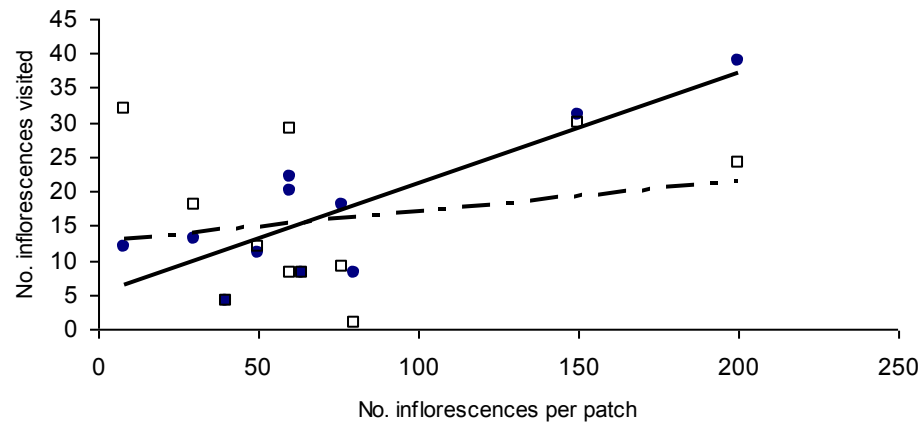


Fig. 2

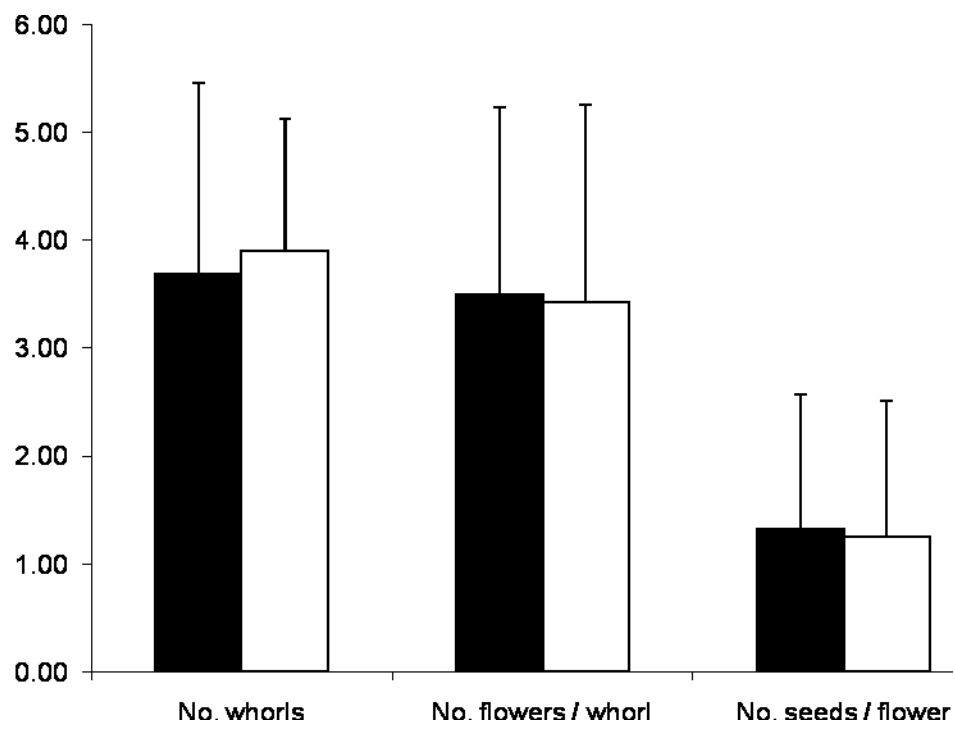




Fig. 3

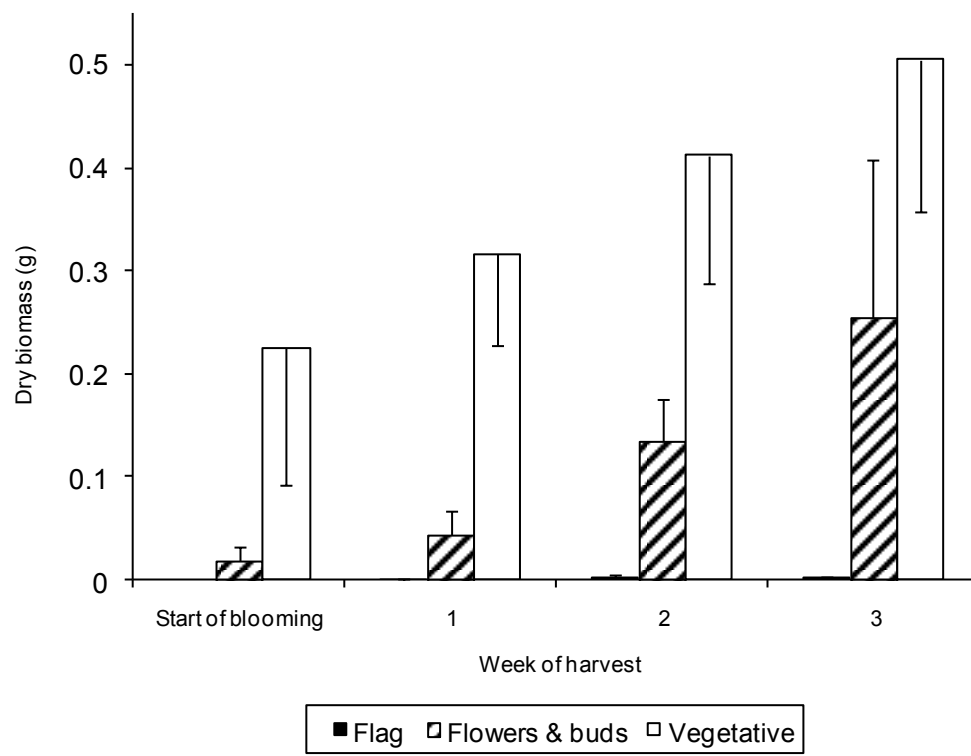


Fig. 4

