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ORIGINAL PAPER

Foliar damage modifies floral attractiveness to pollinators in *Alstroemeria exerens*

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Abstract Pollination is a requisite for sexual reproduction in plants and its success may determine the reproductive output of individuals. Pollinator preference for some floral designs or displays that are lacking or poorly developed in focal plants may constrain the pollination process. Foliar herbivory may affect the expression of floral traits, thus reducing pollinator attraction. Natural populations of the Andean species *Alstroemeria exerens* (Alstromeriaceae) in central Chile show high levels of foliar herbivory, and floral traits show phenotypic variation. In the present field study, we addressed the attractive role of floral traits in *A. exerens* and the effect of foliar damage on them. Particularly, we posed the following questions: (1) Is there an association between floral display and design traits and the number and duration of pollinator visits? and (2) Does foliar damage affect the floral traits associated with pollinator visitation? To assess the attractiveness of floral traits for pollinators, we recorded the number and duration of visits in 101 focal plants. To evaluate the effects of foliar damage on floral traits, 100 plants of similar size were randomly assigned to control or damage groups during early bud development. Damaged plants were clipped using scissors (50% of leaf area) and control plants were manually excluded from natural herbivores (<5% of leaf area eaten). During the peak of flowering, we recorded the number of open flowers, and estimated corolla and nectar guide areas.

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The number and duration of pollinator visits was statistically associated with floral design and display traits. Plants with larger displays, corollas and nectar guide areas received more visits. Visits lasted longer as display increases. In addition, foliar damage affected attractive traits. Damaged plants had fewer open flowers and smaller nectar guide areas. We conclude that foliar damage affects plant attractiveness for pollinators and hence may indirectly affect plant fitness.

Keywords *Alstroemeria* · Floral traits · Herbivory · Indirect effects · Plant–animal interaction · Pollination

Introduction

Pollination is a requisite for sexual reproduction in plants (Dafni 1992), and its success may determine the reproductive output of individual plants. Pollinator availability may constrain the pollination process (Wilcock and Neiland 2002). This limitation can occur due to low abundance of pollinators or as a result of pollinator preference for certain floral designs or displays absent—or poorly developed—in a focal plant (Stanton et al. 1986; Møller and Ericksson 1995; Johnson and Dafni 1998). The relationship between floral traits and pollination success has been largely studied in terms of pollinator response to plant morphological variation and subsequent fitness consequences for plants (Galen 1985; Stanton et al. 1986; Campbell et al. 1991; Johnston 1991; Johnson et al. 1995; Pellmyr 2002). Considerable evidence reports that pollinator behaviour affects reproductive success of plant species that require agents for pollen export or receipt (Schemske and Horvitz 1984; Herrera 1987; Conner et al. 1995; Olsen 1997; Anderson et al. 2005). Floral design and display traits that may be attractive cues for pollinators include corolla size, flower colour, nectar guides, number of open flowers per plant, corolla chemical profile and type of floral symmetry (Galen and Newport 1987; Møller and Eriksson 1995; Conner and Rush 1996; Medel et al. 2003). Extrinsic factors may also affect individual attractiveness for pollinators. For instance, the degree of isolation, i.e., the distance of a focal plant to neighbour plants, is often negatively associated with individual attractiveness (Dafni 1992; Celedón-Neghme et al. 2007).

Foliar herbivores can affect negatively plant fitness components (Bergelson and Crawley 1992; Marquis 1992; Juenguer and Bergelson 2000). Tissue damage caused by herbivores can reduce resource availability to form reproductive structures in the plant (Zamora et al. 1999). Several theoretical and empirical studies show how herbivory can affect the expression of floral traits traditionally associated with plant–pollinator interactions, the “attractive” floral traits. Plants suffering leaf damage show smaller corollas and petals (Aizen and Raffaele 1996; Strauss et al. 1996; Lehtilä and Strauss 1997; Mothershead and Marquis 2000), fewer open flowers at a given time (Karban and Strauss 1993; Strauss et al. 1996; Juenger and Bergelson 2000; Mothershead and Marquis 2000; Elle and Hare 2002; Gómez 2003; Sharaf and Price 2004), displacement of flowering phenology (Strauss et al. 1996; Juenger and Bergelson 1997; Sharaf and Price 2004), and reduction in the concentration of attractive chemical compounds in the corolla (Euler and Baldwin 1996). Furthermore, herbivores may affect the expression of mating systems (Steets et al. 2006, 2007). Changes in pollinator behaviour following modifications in flower morphology induced by foliar herbivory are one of the mechanistic explanations linking foliar herbivory and the expression and evolution of plant mating systems (Steets et al. 2007).

In non-autogamous species, i.e., plants that obligatorily require a pollinator agent to transport pollen from anthers to stigmas, factors affecting pollinator behaviour may determine the reproductive success of individuals. This is particularly important in stressful environments, where pollinator activity is constrained and pollen limitation may occur (Ashman et al. 2004). *Alstroemeria exerens* (Alstromeriaceae) is a protandrous self-compatible but non-autogamous species (Rougier 2005) distributed in the high Andes of Chile and Argentina (Muñoz and Moreira 2003). The more frequent floral visitors of *Alstroemeria* species are Hymenopteran insects (Arroyo et al. 1982; Aizen and Basilio 1998; Cavieres et al. 1998; Botto-Mahan and Ojeda-Camacho 2000). Hymenopterans generally choose flowers or plants to visit based on visual cues such as floral design and display traits (Spaethe et al. 2001). Natural populations of *A. exerens* in Central Chile Andes show high levels of foliar herbivory by Lepidopteran larvae (Suárez et al. unpublished). Although the effects of herbivory on floral traits have been addressed in several studies (cited above), the factual relationship between floral traits affected by herbivores and pollinator preferences is often assumed but seldom demonstrated. The functional relationship between floral traits and pollinator behavior varies with local environmental conditions, which affect both the plant population and the assemblage of associated pollinators. This field study addressed the attractive role of floral traits in *A. exerens* and the effect of foliar damage on them. Particularly, we posed the following questions: (1) Is there an association between floral display and design traits and the number and duration of pollinator visits? and (2) Does foliar damage affect the floral traits associated with pollinator visitation? We also evaluated whether the floral traits are equally attractive for different pollinator species.

Materials and methods

Study species

Alstroemeria exerens (Alstromeriaceae) is a perennial herb that inhabits rocky sites above 1,900 m a.s.l. through the Chilean and Argentinean Andes, between 33°18’ S and 36°04′ S (Muñoz and Moreira 2003). *Alstroemeria* species are perennial plants—rarely annuals—that have both sterile and fertile erect shoots. All Chilean *Alstroemeria* species have zygomorphic flowers, with a homochlamydeous perianth composed by six tepals, arranged in two verticils, in an umbelliform inflorescence. The external verticil of *A. exerens* is composed by almost identical tepals in form and colour (pink). In the internal verticil tepals are generally narrower, with dark lines in a yellow background that have been considered as nectar guides because the nectaries are located in their base. *A. exerens* is a protandrous species, i.e., after some days in the staminate phase (male) the flower enters the pistillate phase (female). Thus, although *A. exerens* is a self-compatible species, it requires pollinating agents for an effective fertilization (Rougier 2005). There is no report about specific pollinating agents of *A. exerens*, but hymenopterans are the most common visitors in other *Alstroemeria* species from Chile and Argentina (e.g. *Alloscirtetica gayi*, *Anthidium funereum*, *Bombus dahlbomii*, *Megachile semirufa*, species of Apoidea and Panurdidae families; Arroyo et al. 1982; Aizen and Basilio 1998; Cavieres et al. 1998; Botto-Mahan and Ojeda-Camacho 2000).

Populations of *A. exerens* in Central Chile show high levels of foliar damage caused mainly by Lepidopteran larvae of the Psychidae and Pieridae families. A 97% of individual plants have some level of foliar damage. Plants show a 50.4 ± 2.8% (mean ± SE) of their leaves with damage signals (sample size = 200 plants; Suárez et al. unpublished data). The study population is located at Farellones (Andes of Central Chile; 33°21′30″ S; 70°18′15″ W; 2,382 m a.s.l) in rocky sites of north-facing (equatorial) slopes. It forms large and conspicuous patches surrounded by a vegetation matrix that includes *Berberis empetrifolia* (Berberidaceae), *Mutisia rosea* (Asteraceae) and *Convolvulus demissus* (Convolvulaceae) as the most common plant species.

Pollinator observation

To assess the attractiveness of floral display and design traits for pollinators, we recorded the number of visits per plant and time spent per plant in each visit (visit duration) in 101 focal plants of *A. exerens*. This was done during the peak of flowering in the 2005 austral summer (December 2004–January 2005). Number of visits and time spent per plant are components of the pollinator foraging behaviour (Dafni 1992). The identity of pollinator taxa was preliminary determined visually. The observations of pollinator visits were conducted by three observers that completed 108 periods of 30 min over 3 days, thus totalling 3,240 min of observation time. Observations were carried out between 09:00 and 17:00; this time period was set after preliminary inspections of pollinator activity in the study population. We considered the number of open flowers, corolla area and nectar guide area as display and design floral traits potentially attractive for pollinators. During observation time, we counted the number of open flowers and recorded the floral phenotype as a digital image for all focal plants. We took at least three pictures per plant when plants had three or more flowers open. When plants had less than three open flowers, all of them were photographed. Given that observations were carried out during flowering peak, and that the growing season is rather short in this high altitude site, the number of open flowers per plant includes most of the flowers that are produced during the season. The corolla and nectar guide areas were estimated from the digital images of each flower using SIGMA SCAN® software, and were analysed as average values per plant. We also classified the isolation level of individuals (distance between flowers of the focal plant and the nearest neighbour plant) using four categories: 1 (1–5 cm), 2 (5–20 cm), 3 (20–30 cm), and 4 (>30 cm). At the end of the observation period pollinators were collected for further identification.

Effect of foliar damage on floral phenotype

In the same season (2005 austral summer), during early bud development, 100 plants of similar size (approximately 30 cm height) were marked and randomly assigned to one of the two groups: control or damage treatment (N = 50 per group). We did not detect initial differences between groups in plant height (ANOVA $F_{1,96} = 0.073$; $P = 0.787$), number of leaves ($F_{1,96} = 0.626$; $P = 0.430$) or number of buds ($F_{1,96} = 0.163$; $P = 0.687$). Plants of the damage group were clipped using scissors (50% of leaf area). In the control group herbivores were excluded continuously during the experiment, picking them off by hand twice a week. This exclosure method allowed levels of damage lower than 5% of total leaf area (estimated by eye). Seven weeks after clipping was applied, during the peak of flowering time, we recorded the number of flowers open and took pictures of flowers in each damaged and control individual plant. Corolla area and nectar guide area were estimated as described above.

Plants may respond differently to artificial damage and natural herbivory. However, the use of natural herbivores is not free of problems. For instance, if larvae are confined on plants in the field, differences in the actual damage imposed may arise from differences in larval feeding behaviour or due to natural enemies. If natural damage patterns are used instead, there could be a bias resulting from an unmeasured biotic or abiotic microenvironmental variable that affects both plant traits and herbivory density or preference. The use of artificial damage, assuming that experiments are properly randomized, avoids these problems and homogenizes the magnitude of damage (Tiffin and Inouye 2000). Nevertheless, because natural and artificial damage are not equivalent, when drawing conclusions it must be kept in mind that results might not be totally representative of a natural situation.

Statistical analyses

The attractiveness of display and design floral traits was evaluated using a Spearman correlation analysis between each trait and both the number and duration of visits per plant. We did not use regression analysis because the pollinator data could not be adjusted to a normal distribution even after applying data transformations. In order to explore whether the more important pollinators showed similar patterns of preference, the analyses were also performed separately for each of the three more frequent visitors in the population.

To evaluate the effect of foliar damage on floral display and design traits, multivariate analysis of variance (MANOVA) was used. The MANOVA approach was used because some of the studied traits were correlated over the $r = 0.80$ conventional threshold for statistical independence (corolla area and nectar guide size; Spearman correlation analysis; $r_s = 0.87$; $P < 0.05$). This analysis is more powerful than univariate ANOVAs because it incorporates several response variables at the same time and accounts for correlated variables (Scheiner 1993). If the MANOVA showed significant effects, univariate ANOVAS were performed to decompose the results and interpret them. The only factor included in all models was the damage status.

Results

The floral design and display traits of *Alstroemeria exerens* showed an important phenotypic variation (CV % = [37.5–43.5]; Table 1). We recorded a total of 324 visits by pollinators. The assemblage of diurnal visitors was composed mostly by Hymenopterans (6 of 14 taxa) and Dipterans (5 of 14 taxa). The most important visitors—in terms of frequency—were *Bombus dahlbomii* (Bombidae: Hymenoptera), *Megachile* sp. (Megachilidae: Hymenoptera) and *Centris* sp. (Anthophoridae: Hymenoptera). These three species accounted for 76.5% of the total number of visits during the whole observation time: *B. dhalbomii*, 23.5%, visiting 41 of 101 focal plants; *Megachile* sp., 35.9% visiting 58 plants; *Centris* sp., 17.0%, visiting 31 plants. All other taxa did not exceed 3.4% of visits, except by the butterfly *Yramea lathonioides* (Nymphalidae: Lepidoptera), which reached a 7.74% of all visits, but only visiting 4 of the 101 focal plants.

The number of pollinator visits was statistically associated with floral design and display traits (Table 2A), while the time spent per visit was only associated with floral display (Table 2B). Overall, plants with more flowers open, larger corollas, and larger nectar guide areas received more visits and visits lasted longer as floral display increased. The isolation level of the plant in the vegetation matrix was also important for pollinator visitation. The more isolated plants had less frequent visits.

Table 1 Natural variation of floral design and display traits of *Alstroemeria exerens* in the study population (high Andes of Central Chile)

Floral traits	Range of variation	Mean ± 1 SE
Number of open flowers	1–6	2.4 ± 0.09
Corolla area (cm^2)	11.1–58.2	30.4 ± 1.1
Area of nectar guide zone (cm^2)	0.91–9.94	3.86 ± 0.16

N = 101 plants

Table 2 Correlation coefficient (r_s) between floral design and display traits of *Alstroemeria exerens* and (A) number of visits and (B) visit length, considering all pollinators and all plants observed

Floral traits	(A) Number of visits r_s (*P*-value)	(B) Visit length r_s (*P*-value)
Number of open flowers	**0.35 (0.0003)**	**0.22 (0.037)**
Corolla area	**0.31 (0.0021)**	0.13 (0.237)
Area of nectar guide zone	**0.29 (0.0031)**	0.07 (0.549)
Isolation level	**−0.35 (0.0003)**	−0.12 (0.269)

N = 101 plants

The different floral design and display traits were not equally related to the visit behaviour of the three more frequent pollinators considered individually (Table 3). The number of visits by *B. dahlbomii* showed a high correlation with the number of open flowers in the plant, a floral display trait, but not with the floral design traits. The duration of visits by this bumblebee was not related to floral design and display traits or the isolation level of plants. The number and length of visits by the solitary bee *Centris sp*. showed a positive association with the size of corollas and nectar guide areas, but not with the number of open flowers. The number of visits by the solitary bee *Megachile* sp. decreased with the isolation level of the plant, but showed no association with floral design or display traits. The duration of visits by this species was not related to any of the evaluated variables.

Overall, foliar damage affected floral attractive traits in *A. exerens* (MANOVA $F_{3,50} = 3.38$; $P < 0.05$). Both design and display traits were affected separately by leaf clipping. Damaged plants showed fewer open flowers (ANOVA $F_{1,81} = 4.31$; $P < 0.05$) and smaller nectar guide areas ($F_{1,55} = 4.68$; $P < 0.05$). The reduction of corolla area in damaged plants was not statistically significant ($F_{1,55} = 0.94$; $P = 0.33$).

Discussion

Floral design and display traits of *A. exerens* were related to the number and duration of visits of pollinators. Plants with smaller flowers, fewer open flowers and smaller surfaces of nectar guides received fewer visits than those with larger flowers, greater displays and nectar guides. These results are in accordance with previous empirical evidence that reports pollinator preference for flowers with larger displays and/or corolla sizes (Bell 1985; Stanton et al. 1986; Møller and Ericksson 1995; Dafni and Kevan 1997; Johnson and Dafni 1998; Ohashi and Yahara 1998). The response of pollinators to natural variation on nectar guide size at the species level has been scarcely evaluated empirically. For instance, it is frequently assumed that putative nectar guides have an important role as attractive trait, but few studies have actually tested this hypothesis. Medel et al. (2003) reported that

Table 3 Correlation coefficient (r_s) between floral design and display traits of *Alstroemeria exerens* and (A) number of visits and (B) visit length, considering the three more frequent visitors and all visited plants

	(A) Number of visits; r_s (*P*-value)			(B) Visit length; r_s (*P*-value)		
	B. dalhbomii	*Megachile* sp.	*Centris* sp.	*B. dalhbomii*	*Megachile* sp.	*Centris* sp.
Floral design and display traits	N = 41	N = 58	N = 31	N = 41	N = 58	N = 31
Number of open flowers	**0.49 (0.001)**	0.18 (0.178)	0.26 (0.159)	0.27 (0.090)	0.24 (0.071)	−0.03 (0.856)
Corolla area	0.21 (0.196)	0.20 (0.135)	**0.51 (0.003)**	0.27 (0.089)	0.11 (0.410)	**0.50 (0.004)**
Area of nectar guide zone	0.15 (0.370)	0.20 (0.129)	**0.45 (0.012)**	0.13 (0.423)	0.18 (0.174)	**0.42 (0.019)**
Isolation level	0.12 (0.456)	**−0.49 (0.0001)**	0.13 (0.493)	−0.12 (0.430)	−0.20 (0.121)	−0.29 (0.108)

the form and size of the nectar guide in a *Mimulus* species (Phrymaceae) is an important floral trait for pollinator attraction, but the specific phenotype preference depends on pollinator identity. With regard to *Alstroemeria* species, Botto-Mahan and Ojeda-Camacho (2000) found that when the nectar guide zone of *A. ligtu* was experimentally removed, flowers were not visited at all. Likewise, Cavieres et al. (1998) found that clipped flowers of *A. pallida*, showing smaller corollas, were less visited by pollinators in the more dense patches of the study population. Therefore, nectar guides and corolla size seem to be attractive signals of importance for pollinators in *Alstroemeria* species. Flowers with larger corollas generally attract more pollinators. This pattern holds at the population as well as at the species level and could be explained by the greater amount of nectar found in larger flowers (Ashman and Stanton 1991; Campbell et al. 1991; Cohen and Shmida 1993). The latter involves the occurrence of associative learning by pollinators foraging for nectar (see Gould 1985 for details) because floral design and display traits may provide a visible cue to locate hidden nectar stocks for pollinators (Cresswell and Galen 1991). Larger flowers might be visual advertisement signals by themselves, not necessarily related to nectar stocks, because they can be seen from longer distances (Cohen and Shmida 1993). This is particularly true when there is a noticeable colour contrast between the flower and the background (Dafni and Kevan 1997; Spaethe et al. 2001). We found that the only frequent visitor that responded to size and colour stimuli in *A. exerens* flowers was the solitary bee *Centris* sp., supporting the idea that different pollinators use different types of signals to select flowers. Floral display influenced *A. exerens* pollinator behaviour. Plants with a greater number of open flowers were more visited and visits lasted longer, as has been reported previously for other species (Conner and Rush 1996; Ohashi and Yahara 1998; Karron et al. 2004). The greater flower supply for visitors may lengthen the foraging time within a plant, which could promote geitonogamy, i.e., intra-plant pollination (Snow et al. 1996). Interestingly, the bumblebee *Bombus dahlbomii* preferred plants with greater display but did not stay a longer time on them. Probably, the expected pattern applies to species with greater floral displays than that of *A. exerens*. Finally, our results suggest that population parameters such as plant density and spatial distribution can affect individual plant attractiveness for some pollinators. The number of visits by *Megachile sp.* was correlated only with the isolation level. Thus, this solitary bee moves preferably between closer plants and does not have preferences for a particular floral phenotype.

We found clear effects of foliar damage on the expression of floral design and display traits that are important to attract pollinators of *A. exerens*. Leaf damage caused a reduction of the nectar guide area and of the number of open flowers per plant. In addition, there was a non-significant tendency for damaged plants to show smaller corollas. Similar patterns in which damaged plants show smaller corollas and/or displays than intact ones are well documented for several plant species (Karban and Strauss 1993; Frazee and Marquis 1994; Euler and Baldwin 1996; Strauss et al. 1996; Lehtilä and Strauss 1997; Wisdom et al. 1989; Mothershead and Marquis 2000; Elle and Hare 2002; Gómez 2003), and this is the first report of some effect of foliar herbivory on nectar guide size. Particularly considering *Alstroemeria* species, Aizen and Raffaele (1996) found that artificial defoliation caused a reduction in tepal length and in nectar quality, but not in nectar quantity, in *A. aurea*. These results are in accordance with our findings since they show negative effects of damage on floral traits potentially attractive for pollinators. The mechanisms underlying the herbivory-induced modification of floral traits are still unknown. The most parsimonious explanation is that the observed phenotypic modifications might be a consequence of resource shortage due to the decrease of photosynthetic surface in the plant. Alternatively, they might be the result of a trade-off between resource allocation to reproductive traits and compensatory responses to foliar loss, or anti-herbivory defences. This is an interesting research line that remains scarcely explored.

Although pollinator activity was not evaluated in the cited study on *A. aurea* (Aizen and Raffaele 1996), the authors did not find an effect of damage on pollen export and deposition, which are male fitness components. Earlier work in other systems has also failed to show herbivory effects on plant fitness through a decrease in pollinator visitation (Hambäck 2001). Behaviour of *A. exerens* visitors was significantly associated with floral trait variation, but their efficiency as pollination agents has not been determined. We also lack data on the fitness consequences of pollinator visitation for *A. exerens*. Nevertheless, the fitness consequences of changes in pollinator visitation induced by foliar herbivory should be important in this non-autogamous high Andes species. Many empirical tests indicate that pollen insufficiency often limits seed production (Ashman et al. 2004). Foliar damage may be a sufficient explanation for pollen limitation because decreasing pollinator attraction have negative consequences on mate availability (Knight et al. 2005; Steets et al. 2007), and it may be intensified in high Andes habitats where climate harshness makes the pollination service scarce and/or unpredictable.

Strauss (1997) has described several paths through which foliar herbivory can indirectly affect plant fitness via floral trait expression and pollinator behaviour. Leaf damage in *A. exerens* causes modifications in floral traits that are attractive for pollinators. Therefore, foliar herbivores have the potential to influence the behaviour of floral visitors, hence affecting plant reproductive success. Moreover, if floral traits modified by leaf damage have differential importance for the pollinator species, as results do suggest, then herbivores might modify the pollinator assemblage in this population. Further research should address the mechanistic basis of the observed changes in floral traits caused by foliar damage in *A. exerens*, and assess the relative importance of direct and indirect effects of foliar herbivory on plant fitness.

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