Do flowers wave to attract pollinators? A case study with *Silene maritima*

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floral movement; flower stalk; pollination; *Silene maritima;* stabilizing selection; wavy flowers.

Abstract

To answer the question whether flowers wave to attract pollinators, we determine: (1) the heritability of floral mobility; (2) whether wavy flowers attract more insects; (3) does the duration of pollination affect seed set; and (4) the relationship between seed set and floral mobility. The pollination ecology of Silene maritima was investigated. Flowers on stalks of different waviness were used to investigate the effect of floral movement on pollinator visits. There is heritable variation in both direct and indirect estimates of floral mobility. The highest insect total visitation times were associated with medium length thin stalks that were visited more frequently and by more insect species. Although mean individual visit durations were less than those of less mobile flowers, this was compensated for by increased visits. Observations of controlled pollinations show that when the visit times are low, so is seed set and therefore low and high mobility flowers might suffer from reduced fitness. Combining these observations provides a mechanism that could be driving stabilizing selection for flower stalk traits, with a trade-off applying between waving to attract pollinators and not being too mobile as to prevent effective pollination. Further evidence for stabilizing selection is provided by the relationship observed in the field between seed set and floral mobility where the highest levels of fitness was associated with intermediate levels of floral waving.

Introduction

The flowers of angiosperms are renowned for their high degree of diversity of form. Darwin (1862) was amongst the first to demonstrate the significance of variation in floral design in ensuring successful pollination. Indeed the interactions between floral design and the diversity of insect pollinators are regarded as a classical example of co-evolution which was in part responsible for the adaptive radiation that occurred in both these groups following the end of the Cretaceous (Richards, 1997). Almost every element of the design of flowers has been extensively researched (Proctor *et al.*, 1996) and demonstrated to be important in attracting pollinators. Examples include colour (Heuschen *et al.*, 2005), shape (Nakano & Washi-

tani, 2003), nectar (Smithson, 2002) scent (Mant *et al.*, 2005) and floral display (Naug & Arathi, 2007). In addition to being a prime example of adaptive evolution, pollination strategies and the structure and function of the angiosperm flower are amongst the first ecologies that we study in school. However, one potentially important mechanism linked to the structure of the angiosperm inflorescence may have been overlooked or dismissed in terms of its role in attracting pollinators and this is the waving of flowers. Faegri & van der Pijl (1971) argued that floral movement may be important in smaller flowers, but generally dismissed its significance because they considered the eyes of insects to be highly sensitive to colour but insensitive to movement.

Previously, the function of the flower stalk has been investigated in terms of seed dispersal (Verbeek & Boasson, 1995) and in some species bending of the stalk is thought to be important in protecting the developing flower from rain (Huang *et al.*, 2002). Here, we consider the potential role of the stalk in attracting pollinators by

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facilitating flower waving. This is because within many plant families there are both stalked and nonstalked species (e.g. the Caryophyllaceae, Crassulaceae and Pyrolaceae). Although stalk-less species tend to be associated with exposed alpine habitats (Clapham et al., 1987), some stalked species are found in extremely windy coastal habitats (e.g. Armeria maritima and Silene maritima). If the function of the stalk is purely related to seed dispersal, it raises the question - why do these maritime species not practise post-flowering stalk elongation which is common in many species (Verbeek & Boasson, 1995). This may reduce the likelihood of damage in this extreme environment. Furthermore, if we accept the premise that insects are not highly sensitive to movement, we are still left with the problem - can they effectively visit and pollinate vigorously waving flowers in exposed conditions?

To answer the evolutionary question – do flowers wave to attract pollinators – we need to determine, if there is genetic variation for waviness, that wavy flowers attract more insects and that more visitors results in greater pollination efficiency and ultimately what is the relationship between floral mobility and seed set/fitness. To address these questions, the pollination ecology of *S. maritima* was investigated. Flowers of *S. maritima* mounted on stalks of different lengths and thickness were used to investigate the effect of floral movement on the behaviour of potential pollinators in an exposed coastal habitat. The likely fitness implications of this and the heritability of waviness are also determined.

Materials and methods

Study site and study species

All plant material was derived from and observations of the effect of floral movement were carried out at Tanybwlch Site of Special Scientific Interest, Cardigan Bay, West Wales (52°24'45.15'N and 4°5'24.43'W). The site is a modified sand and shingle spit which stretches southwards for a kilometre from the mouth of the river Ystwyth. In most years, the site supports a large population (> 1000) of isolated plants of S. maritima which together with patches of prostrate Prunus spinosa account for most of the vegetation. The site is extremely exposed; however, the observations were made and the majority of the vegetation was found on the leeward side of the shingle ridge. Silene maritima is a perennial herb with flowering shoots 8-25 cm; it is sometimes considered a subspecies of Silene vulgaris. Its nonflowering stems typically form loose cushions which allow individual plants to be easily identified growing among the shingle. The flowers are white, 20-25 mm in diameter, each flower is surrounded by a bladdery calyx and the flowers are carried in inflorescences typically of one to four flowers. The species is considered to be outbreeding, although it apparently lacks any incompatibility mechanism (Marsden-Jones & Turrill, 1946). Flowers are hermaphrodite and slightly protandrous and occasional female flowers are known (Baker & Dalby, 1980).

Heritability of waviness

In April 2004, stem cuttings were taken from 10 plants of S. martima selected visually. Five plants having short flower stems and five having long stems were selected. These plants were grown outside in a common garden near the field site in pots until May 2005. Then the three plants with the longest flower stalks and three plants with the shortest flower stalks (averaged over all present) were selected. Entire plants were bagged to prevent pollination, seed set in bagged plants was less than two per cent suggesting limited selfing in the absence of pollinators. A crossing programme was carried out in which each of the six parent plants was hand pollinated with each of the other five plants. Each parent plant was used as both female and male parent, but not selfed, giving a total of 30 different crosses. The resulting seeds were sown in the autumn, and 10 progeny plants were grown from each of the 30 crosses, giving a total of 300 progeny plants. The parents and progeny plants were fully randomized and grown outside in pots until June 2006, when the length and mid-point diameter of five flowering stems per plant were measured. In addition, direct estimates of floral mobility were made for all these plants by recording the number of oscillations per minute and the length of the longest oscillation (in cm) per single newly opened flower per plant on five separate days each with low wind conditions. These two values were multiplied and the average of the five observations used as a direct estimate of the plant's floral mobility.

The narrow-sense heritabilities for the two flower stalk traits (as indirect estimates of floral mobility) and the direst estimate of floral mobility were estimated directly using the mid-parent–offspring regression method (Gilbert, 1973). Although this method suffers from a lack of independence of the points in the regression, as each parent is used more than once, it provides a comparative estimate because the method has been widely used to estimate heritabilities and its limitations are well known and documented (Simmonds, 1979; Falconer, 1989).

Field observations of pollinators

During May and June 2005, freshly picked garden-grown (but derived from seed from the study site), newly opened individual flowers of *S. maritima* were attached to artificial stalks measuring: 7.5, 15 (approximating to the average length of 100 stalks measured in the field) or 30 cm with clear adhesive tape. The stalks were made of wire coated in green plastic and measuring 0.75 (thin) or 2 mm (thick) in diameter, giving a total of six treatment combinations of length and thickness. For each stalk, length × thickness treatment, 20 modified flowers

(approximating to the average number of open flowers recorded per patch) were all placed together within isolated cushions of S. maritima from which all other open flowers had been removed. The flowers were left for half an hour before observations of visiting insects were recorded. Observations were made of all visiting insects, the duration of each visit and the number of flowers visited by each insect over a period of 1 h was recorded, before the flowers showed signs of wilting. Ten replicate observations were made per treatment each from a different location separately between 10:00 and 17:00 hours. Replicates were randomized over time. Fresh flowers were used for each set of observations, which were only made on days with less than 50% cloud cover. Immediately after each of the 10 replicates per treatment had been completed, the number of oscillations per minute was recorded visually for a randomly selected individual flower, as the number of times it touched a vertical marker; in addition, the wavelength of the maximum oscillation in that minute was also measured. Similarly, all the above insect behaviour and flower movement measures were also recorded for 10 replicates of patches of 20 intact S. maritima flower stalks again in isolated cushions. For each set of observations, the six stalk treatments were compared using a two-way ANOVA (MINITAB version 12.23; Minitab Inc., PA, USA) (Tables 1 and 2).

Pollination efficiency and seed set

To establish the relationship between pollinator visit duration and efficiency of seed set, a series of controlled duration pollinations were performed with the common hoverfly *Eristalis pertinax*, which was observed to be a regular and amongst the most frequent visitors to the flowers of *S. maritima* at Tanybwlch. It was selected because its large size makes it easy to handle and because it seemed a reasonable representative of the generalist dipteran pollinators that were observed to visit *S. mari*

tima flowers. During June 2005, wild-caught individuals of E. pertinax were used to perform manipulated pollinations of *S. maritima* flowers of fixed time periods. The flies were 'loaded' with pollen by being given unrestricted access to caged S. maritima donor plants in full flower for a period of at least 1 h. Individual flies were then removed and introduced to uncaged receptive flowers that had previously been emasculated and bagged. Flower visit durations were restricted by 'startling' the flies after the following time periods: 10, 20, 30, 40, 50 and 60 s. Visits over 90 s were pooled into a long visit class. Each time period was replicated 10 times, with individual flowers and flies, giving a total of 70. After pollination, the flowers were rebagged and the seed allowed to develop for 3 weeks before the number of full and empty seeds produced was recorded.

To investigate the relationship between floral mobility and seed set, 100 wild plants were randomly selected at the Tanybwlch. For each of these plants, two flowers on the point of opening were tagged with green cotton. Any other flowers or buds on the same stalk were removed and stem lengths, widths and floral mobility were all estimated as above (on a single occasion for each of the 200 flowers) during June 2006. After flowering was complete, the tagged flowers were left for a further 3 weeks before being harvested and, as above, the number of full and empty seeds recorded. Percentage seed set per flower was then plotted against both the direct estimate of floral mobility and against an indirect estimate of floral waviness (stalk length/stalk mid-point diameter; Fig. 2; the polynomial equations were fitted using Microsoft Excel).

Results

Heritability of waviness

Using the mid-parent–offspring method, the regression coefficient obtained by regression of the mean off-spring

Table 1 Mean total numbers of flowers visited per hour (SD), mean durations of flowers visits (s) (SD), mean number of different species to visit flowers per hour (SD), mean number of flower oscillations per hour (SD), mean maximum wavelength (cm) values are based on 10 replicates per stalk treatment.

Observation	Stalk thickness (mm)	Short (7.5 cm)	Medium (15 cm)	Long (30 cm)	Intact flower stalks
Total number of visits	Thick (2)	4.4 (1.07)	7.7 (1.83)	3.4 (0.97)	25.1 (10.00)
	Thin (0.75)	13.1 (2.47)	17.4 (4.67)	4.8 (1.31)	
Duration of visits (s)	Thick (2)	8.0 (2.28)	4.3 (0.94)	4.9 (2.06)	4.7 (2.19)
	Thin (0.75)	2.6 (1.67)	3.7 (1.71)	1.1 (0.37)	
Total duration of visits (s)	Thick (2)	35.2	33.1	16.7	118.0
	Thin (0.75)	34.1	64.4	5.3	
Number of species of visitors	Thick (2)	2.0 (0.82)	2.4 (0.84)	3.0 (0.94)	7.1 (1.91)
	Thin (0.75)	3.8 (1.03)	6.1 (1.37)	2.4 (0.83)	
Oscillations per minute	Thick (2)	3.5 (3.84)	9.0 (4.21)	53.3 (21.47)	35.9 (15.05)
	Thin (0.75)	25.8 (12.05)	32.8 (9.31)	66.9 (18.91)	
Max wavelength (cm)	Thick (2)	0.18 (0.17)	0.55 (0.25)	1.35 (0.41)	1.7 (0.42)
	Thin (0.75)	0.56 (0.22)	1.47 (0.35)	4.6 (0.77)	. ,

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Table 2 Results of two-way analysis of variance of total numbers of flowers visited per hour, durations of flowers visits, mean number of different species to visit flowers, number of flower oscillations per hour, maximum wavelength, values are based on 10 replicates (of patches containing twenty modified flowers) per stalk treatment.

No. of visits Thickness 1 653.40 111.73 < 0.001 Length 2 358.22 61.25 < 0.001 Interaction 2 102.65 17.55 < 0.001 Error 54 5.85 0.001 Duration Thickness 1 159.41 58.89 < 0.001 Length 2 25.66 9.48 < 0.001 Length 2 29.53 10.91 < 0.001 Error 54 2.71 No. of species Thickness 1 40.02 40.54 < 0.001 Length 2 14.21 14.40 < 0.001 Length 2 12.32 < 0.001 Interaction 2 23.21 23.52 < 0.001 Length 2 $12.138.0$ 67.23 < 0.001 Length 2 151.6 0.84 0.437	Source	d.f.	MS	F	Р
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Error 54 5.85 Duration Thickness 1 159.41 58.89 < 0.001	Interaction	2	102.65	17.55	< 0.001
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No. of species Thickness 1 40.02 40.54 < 0.001	Error	54	2.71		
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Length 2 14.21 14.40 < 0.001 Interaction 2 23.21 23.52 < 0.001	Thickness	1	40.02	40.54	< 0.001
Interaction 2 23.21 23.52 < 0.001 Error 54 0.99 </td <td>Length</td> <td>2</td> <td>14.21</td> <td>14.40</td> <td>< 0.001</td>	Length	2	14.21	14.40	< 0.001
Error540.99OscillationsThickness15940.232.90< 0.001	Interaction	2	23.21	23.52	< 0.001
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Thickness 1 5940.2 32.90 < 0.001 Length 2 12 138.0 67.23 < 0.001	Oscillations				
Length 2 12 138.0 67.23 < 0.001 Interaction 2 151.6 0.84 0.437 Error 54 180.5 Wavelength Thickness 1 34.50 200.97 < 0.001	Thickness	1	5940.2	32.90	< 0.001
Interaction 2 151.6 0.84 0.437 Error 54 180.5 Wavelength	Length	2	12 138.0	67.23	< 0.001
Error54180.5WavelengthThickness134.50200.97< 0.001	Interaction	2	151.6	0.84	0.437
Wavelength 34.50 200.97 < 0.001 Length 2 36.86 214.67 < 0.001	Error	54	180.5		
Thickness 1 34.50 200.97 < 0.001 Length 2 36.86 214.67 < 0.001	Wavelength				
Length 2 36.86 214.67 < 0.001 Interaction 2 11.63 67.75 < 0.001	Thickness	1	34.50	200.97	< 0.001
Interaction 2 11.63 67.75 < 0.001 Error 54 0.17	Length	2	36.86	214.67	< 0.001
Error 54 0.17	Interaction	2	11.63	67.75	< 0.001
	Error	54	0.17		

value on the mid-parental values is used as a direct estimate of the narrow-sense heritability (h^2) of the trait (±SE). Both stem traits were found to have significant narrow-sense heritability values (stem length 0.36 ± 0.02 and stem diameter 0.25 ± 0.01). Similarly, the direct estimate of floral mobility was found to have a low but significant (h^2) value of 0.23 ± 0.11 . Separate regression analyses were performed on mean offspring values on both female and male parental values. This produced very similar heritability estimates, indicating no significant maternal effects and confirming that the phenotypic variance of the two sexes were of similar magnitude. The female parental heritabilities for stem length, diameter and floral mobility were 0.41 ± 0.02 , 0.31 ± 0.01 and 0.24 ± 0.11 , respectively, and those derived from the male parents being 0.32 ± 0.04 , 0.22 ± 0.02 and 0.19 ± 0.12 .

Field observations of pollinators

Flowers mounted on thin stalks (0.75 mm) were observed to be significantly more mobile than flowers on thick stalks (2.00 mm). Pooled over length, thin stalks were found to oscillate about twice as many times per minute than did thick stalks (41.83 compared with 21.93

times respectively). Moreover, pooled over length, thin stalks were observed to have a maximum wavelength about three times that of thick stalks (2.21 cm compared with 0.69 cm respectively). The more mobile flowers mounted on the thin stalks were found to be visited more frequently, but for less time than were flowers mounted on thick stalks, again pooled over stalk length (a mean of 11.76 flowers on thin stems were visited per hour for, on average, 2.5 s compared with 5.1 flowers on thick stalks being visited for, on average, 5.7 s). Tables 1 and 2 reveal many significant interactions, for example, flowers on long thin stalks appear relatively less attractive than other flowers on thin stalks and were visited for shorter periods than all other treatments. Flowers mounted on medium length thin stalks appeared to be most similar to the intact flowers, both in terms of their waviness and their insect visitors.

Pollination efficiency and seed set

The efficiency of seed set was observed to increase with the duration of pollination (see Fig. 1). With approximately 95% of seed set being attained with pollination times above 2 min in duration. Pollination times of less than a minute's duration were associated with reduced levels of seed set and higher levels of variation in seed set efficiency.

Four per cent of the tagged open pollinated wild flowers could not be relocated after 3 weeks; however, sufficient remained to reveal that maximum seed set rates were associated with intermediate levels of floral mobility (however, this was estimated) (see Fig. 2). The relationship between the direct estimate of floral mobility and seed set was best represented by a third-order polynomial equation (Fig. 2a), as determined by calculation of Akaike's information criterion (AIC) (Akaike, 1974), whereas the lowest value of AIC was found to



Fig. 1 Relationship between the mean duration of pollination visit and mean percentage of seed set. Error bars are \pm SD, the second-order polynomial trend-line equation and r^2 values were produced using Microsoft Excel.



Fig. 2 (a) Relationship between percentage of seed set and the direct estimate of floral mobility measured in 100 wild plants. The third-order polynomial trend-line equation and r^2 values were produced using Microsoft Excel. (b) Relationship between percentage of seed set and the indirect estimate of floral mobility (stem length/width) measured in 100 wild plants. The second-order polynomial trend-line equation and r^2 values were produced using Microsoft Excel.

be associated with a second-order polynomial for the relationship between the indirect estimate of mobility and seed set (Fig. 2b). In both cases, there were highly significant regression coefficients (P < 0.001) and r^2 values close to 0.5.

Discussion

Although the importance of the flower stalk in dispersing seeds has long been known (Salisbury, 1942; Verbeek & Boasson, 1995), the results presented here strongly suggest that its adaptive significance as a mechanism for attracting pollinating insects by facilitating floralwaving has been overlooked. The results presented in Tables 1 and 2 show that mobile flowers are visited more frequently and by more species than are the more stable flowers. Although average visit durations were less in mobile flowers, this was more than compensated for by the increased number of visits, so that the highest total visit times were associated with intermediately mobile flowers. The most highly mobile flowers were seen to attract fewer pollinators for shorter durations and therefore were associated with reduced total visit times. Figure 1 demonstrates that such short pollination times

are likely to result in reduced seed set and hence in reduced fitness. Therefore, the most mobile and stable flowers are likely to have reduced pollination efficiencies. When these observations are combined with the narrowsense heritability estimates of floral mobility (either indirectly as stalk length and diameter or as the direct estimate of floral mobility), these provide evidence for a significant genetic component to variation in floral waviness, and potentially a mechanism which could be driving stabilizing selection in the evolution of floral waving. The relationship observed in the field between floral mobility and seed set in Fig. 2 is not tight, but this again provides more evidence for stabilizing selection, with the highest levels of seed set being associated with intermediate levels of floral mobility. However, this relationship could also arise from unfit plants having both short immobile flower stalks and low seed set levels for reasons completely unrelated to pollinator attraction. Similarly, highly mobile flowers may also be indicative of physiological problems.

The narrow-sense heritability estimates of the various estimators of floral mobility were all rather low. This may be because of the large potential for environmental influence of variable wind speeds, etc. plus genetic variation for other traits effecting floral mobility has not been accounted for, such as floral size and design. Alternatively, the low heritability estimates could be seen as evidence that selection on the floral mobility has removed much genetic variation from the population. Overall, the wild sampled flowers' regression revealed a significant linear relationship between stem length and width $r^2 = 0.46$ (with longer stems tending to be thicker); however, combining these two stem traits into a single indirect estimate of mobility appears to have captured something biologically meaningful.

The flowers mounted on longer and thinner wavy stalks were observed to attract more pollinators, but these most mobile flowers appeared to be too difficult for the insects to visit for any length of time and Fig. 1 suggests that this will reduce pollination efficiency (Conner et al., 1995). It seems likely that this trade-off between waving to attract pollinators and not being too mobile as to prevent effective pollination was responsible for the flowers on the medium length, thin stalks attracting most insects and being most similar to the flowers on their own intact stalks. The observation that insects are attracted by movement and not just colour is consistent with the discovery of motion-sensitive neurons in insects (Ibbotson, 2001). The extent of the highly significant differences observed in insect behaviour is perhaps not surprising given the great differences seen in mobility between the different stalk treatments. This may indicate that the treatments were too extreme to represent reality; however, in the field, real flowers were observed to be highly variable in their mobility (spanning the range of the artificial stalks) which is reflected in the high standard deviations presented in Table 1. This in turn

may be related to the fact that natural variation in stalk length is similar to the artificial stalk treatments (Clapham *et al.*, 1987).

The simple observations presented here raise a number of questions about the role of flower waving in attracting pollinators. For example, do plants modify the waviness of their flowers during development in such a way as to enhance the overall attractiveness of a patch of flowers (with a patch equating to a single genet), while allowing individual flowers to be less wavy (and hence increasing the visits durations) when they are receptive? Parallels to this are known in flower colour change (Weiss, 1995) in which the attractiveness of the overall inflorescence is maintained, whereas that of an individual flower is reduced by changes in colour once it is no longer receptive. For such a mechanism to work with floral movement would require considerable flower-to-flower variation in waviness, which is compatible with the high degree of variance observed in waviness of flowers on their own intact stalks (Table 1). Flower shape and form are also likely to effect floral mobility, but here the tradeoffs are likely to be much more complex than those relating to stem construction.

A further complication that arises from our results is that individual species of pollinator must vary in their ability to land on and move in mobile flowers and effectively transfer pollen. Therefore, the nature of the trade-off between waving to attract pollinators and being too mobile to facilitate pollination is likely to be plant/pollinator specific. The hoverflies used in our manipulated pollinations are among the larger species to visit *S. maritima* and so there is probably little value in comparing the seed set results in Fig. 1 with the estimated total visit times in Table 1. Although our observations are limited to a single species of plant at one location, we feel that they do open up many such new questions in what appears to have been a neglected aspect of pollination evolutionary ecology.

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