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Why do bilaterally symmetrical flowers orient vertically? Flower orientation influences pollinator landing behaviour

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ABSTRACT

Flower orientation is an important character influencing plant fitness. Zygomorphic flowers are known to orient vertically. We conducted field experiments in which we changed the flower angle of zygomorphic *Commelina communis* to determine how flower orientation affects pollinator behaviour. We confirmed that *Commelina* flowers oriented vertically like other zygomorphic flowers. Then, we artificially prepared control, upward- and downward-oriented flowers and exposed them to natural pollinators (syrphid flies and bumblebees). We found that the frequency of approach by syrphid flies and bumblebees was not influenced by flower angle, but there were fewer landings on downward-oriented flowers than on control and upward-oriented flowers. Moreover, the upward flower orientation increased illegitimate landings (landing on the flower without touching the stigmas or mating-related anthers) compared with controls. Thus, vertical flower orientation in zygomorphic flowers serves to control pollinator landings. Our findings suggest that deviations from vertical orientation may reduce fitness in *C. communis* by reducing the efficiency of insect-mediated pollen transfer.

Keywords: *Commelina communis*, field experiment, flower orientation, pollinator landing, zygomorphic flower.

INTRODUCTION

Flower orientation, which is an inherited character in some species (Hodges *et al.*, 2002), is considered to be an adaptation to the abiotic or biotic environment (Hocking and Sharplin, 1965; Kevan, 1975; Kudo, 1995; Tinoco-Ojanguren and Molina-Freaner, 2000; Huang *et al.*, 2002; Patino *et al.*, 2002; Galen and Stanton, 2003). For example, downward flower orientation is thought to have evolved to avoid pollen damage and nectar dilution by rainfall (Huang *et al.*, 2002; but see Tadey and Aizen, 2001), while upward orientation towards the sun (i.e. flower heliotropism) increases internal flower temperature, which in turn promotes pollinator attraction, pollen tube growth and seed

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maturation in some arctic and alpine species (Hocking and Sharplin, 1965; Kevan, 1975; Kudo, 1995; Galen and Stanton, 2003; see also the case for tropical flowers, Patino *et al.*, 2002).

Unlike radially symmetrical (actinomorphic) flowers, the *en face* surface of bilaterally symmetrical (zygomorphic) flowers is usually either vertical or oblique (inclined or declined) (see Neal *et al.*, 1998, and references therein; Giurfa *et al.*, 1999). Neal *et al.* (1998) suggested that this vertical orientation restricted the approach direction of visiting insects to facilitate their recognition of complex floral patterns. In this sense, the vertical orientation in zygomorphic flowers is thought to have co-evolved with insect recognition ability and would increase pollinator revisitation (Neal *et al.*, 1998; Giurfa *et al.*, 1999).

Flower orientation may also affect pollinator landing behaviour. Compared with actinomorphic flowers, zygomorphic flowers restrict the landing point of pollinators as a consequence of their complex floral structures. Zygomorphic flowers often have specific organs for pollinator landings, such as lower lips (Neal *et al.*, 1998). Changes in flower orientation may impair the function of these organs: we expect that downward orientation reduces the number of landing points, whereas upward orientation enhances landings on floral organs other than landing-specialized organs. This may decrease the number of landings by flower visitors or increase illegitimate landings (i.e. landings without touching mating-related anthers and/or stigmas). An illegitimate landing may induce reward thieving (or robbing) behaviour by flower visitors, which in turn often decreases plant fitness (Inouye, 1980; Maloof and Inouye, 2000; Irvin and Maloof, 2002).

A few experimental studies have examined the effect of flower orientation on pollinator attraction (Tadey and Aizen, 2001; Patino *et al.*, 2002). Experimental examination of how flower orientation controls pollinator landing behaviour after arriving at plants will provide us with information on the evolution of floral orientation. Here, we report an experimental case study of the effects of flower orientation on insect behaviour, especially landing behaviours, in zygomorphic *Commelina communis*. First, we examined whether the orientation of *C. communis* flowers was vertical. Second, we changed the flower orientation experimentally to examine how such changes would affect the approaching and landing behaviours of two types of flower visitors, syrphid flies and bumblebees. Finally, we discuss the significance of vertical flower orientation in zygomorphic *Commelina* flowers for controlling pollinator behaviours.

MATERIALS AND METHODS

Study species

Commelina communis L. (Commelinaceae) is an annual, andromonoecious herb of disturbed areas that is widely distributed in temperate north-east Asia, often growing around rice fields and along roads. One plant usually has many inflorescences, in which perfect flowers bloom before staminate flowers. A single inflorescence usually has four flower buds per bract. In most cases, a single flower per inflorescence opens at sunrise each day and lasts until noon. Ushimaru *et al.* (2003a) found that large blue petals are larger in perfect flowers (11.8–13.9 mm mean length) than in staminate flowers (10.6–13.0 mm) in eight natural populations.

The flower has three types of stamen: two long brown stamens (10.8–12.1 mm mean filament length), one medium-length yellow stamen (5.2–7.2 mm) and three short yellow

stamens (2.9–4.5 mm). The anthers of long (L-anther) and medium-length (M-anther) stamens produce fertile pollen; the anthers of short stamens (S-anther) produce only a small amount of sterile pollen and are only for display (Morita and Nigorikawa, 1999). M-anthers produce fewer pollen grains on average ($n = 2000$) than do L-anthers ($n = 3500$) (Morita and Nigorikawa, 1999). *Commelina communis* flowers do not bear nectar, and pollen is the only floral reward for their pollinators. Pollen from L-anthers contributes to outcrossing, whereas pollen from M-anthers functions mainly as a reward for pollinators visiting this nectarless species (Morita and Nigorikawa, 1999).

In *C. communis*, the filaments of long stamens are typically elongate, and they seem to function as a kind of landing platform (Fig. 1), which is often not true of other *Commelina* species, such as *C. diffusa* and *C. erecta*. The length of the long stamen and style was less variable than that of other floral organ sizes in perfect flowers (Ushimaru *et al.*, 2003a), and the correlation between them was the strongest among all floral correlations (Ushimaru *et al.*, 2003b). These facts suggest that the position of fertile stigmas evolved to maximize receipt from pollinators of pollen grains from L-anthers of the same height in perfect flowers (Ushimaru *et al.*, 2003a,b).

Commelina communis is self-compatible and can experience delayed autogamy and bud pollination (Morita and Nigorikawa, 1999). The pistils and long stamens roll up at the end of anthesis, stimulating autonomous self-pollination through L-anther–stigma contact (Morita and Nigorikawa, 1999). However, the high ratio of pollen per ovule (2100–2500), which is higher than that for facultatively xenogamous species (Cruden, 1977), in perfect flowers and the existence of staminate flowers indicate that pollinator-mediated outcrossing occurs in this species (Morita and Nigorikawa, 1999). Syrphid flies (Syrphinii species) are the main flower visitors of *C. communis* in most cases; bee species, such as bumblebees, honeybees and small solitary bees, sometimes visit *Commelina* flowers (Tanaka, 1978; Ushimaru *et al.*, 2003a,b; A. Ushimaru, T. Watanabe and K. Nakata, unpublished data).

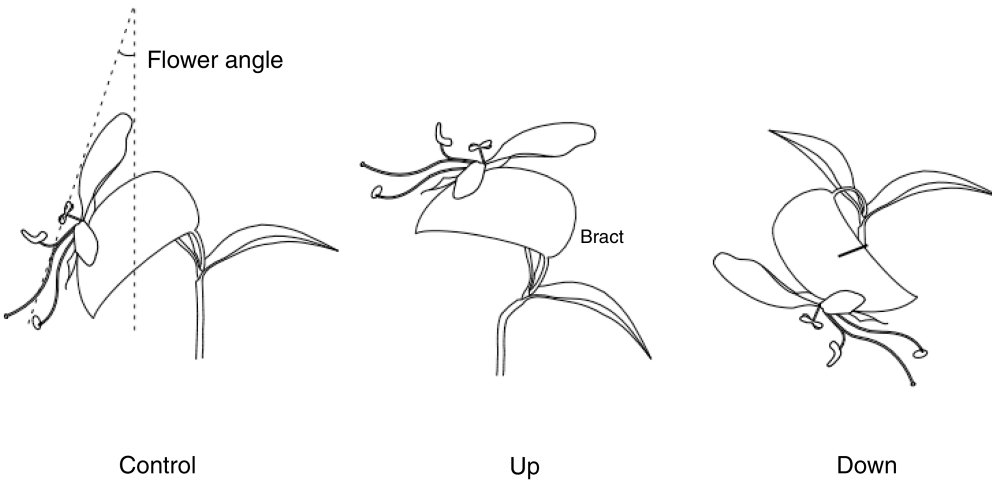


Fig. 1. Side views of Control, upward-oriented (Up) and downward-oriented (Down) flowers. Bracts of Down flowers were fixed by staples.

Flower orientation

We examined the natural flower orientation of *C. communis* by measuring flower angle with a clinometer (Showa Sokki Co., Tokyo, Japan) in 2003 (Fig. 1). We haphazardly selected 40 flowers at Ohara (35°08′ N, 135°50′ E) and 50 at Yamanaka (35°02′ N, 135°49′ E) in Kyoto City and measured their flower angles.

Field experiment

On 7, 9 and 11–13 September 2003, we conducted a field experiment with an Ohara population in which syrphid flies (mainly *Episyrphus balteatus*) and a bumblebee species, *Bombus diversus* Smith, visited *Commelina* flowers. We prepared the following three types of flowers experimentally and exposed them to natural pollinator visitations (Fig. 1):

- *Control*: intact flowers for controls (flowers with angles of 0–20°);
- *Up*: flowers whose faces were turned upward; and
- *Down*: flowers facing downward.

It was technically difficult to change the stalk angle of an individual flower inside a bract. Therefore, we leaned the plant stems and fixed them to prepare Up flowers, and we bent the inflorescence stalks with staples to prepare Down flowers (Fig. 1); the flower angles of these flower types were approximately 90° and −90°, respectively. We often removed leaves that decreased the space in front of Down flowers.

For each trial, we arbitrarily chose a flower patch (containing more than six flowers in 50×50 cm) and haphazardly selected 5–7 flowers inside the patch. We manipulated these flowers (6 flowers: 2 Control, 2 Up and 2 Down, in most cases) and observed pollinator behaviours (approach and landing behaviours) on these flowers for 15 min. We used only perfect flowers for the trials to exclude sex differences in flower size. We made all observations in the morning (06:30–09:30 h). For each trial we used a new patch of flowers. We conducted 30 trials (4–8 trials per day) during the experimental period; in total, 180 flowers were examined (70 Controls, 57 Up and 53 Down flowers).

Pollinator behaviour and landing type categorization

First, we recognized two pollinator behaviours: approach and landing. Approach occurred when pollinators found flowers and approached them from the front. Landing occurred when pollinators landed on any part of a flower after approach behaviour. We further categorized pollinator landings into the following five types:

1. *Legitimate landing*: pollinators held onto the filaments of L- and M-anthers or a small white petal and foraged or collected pollen grains from the M-anther, while simultaneously touching the L-anthers or stigma with their abdomens (Fig. 2).
2. *M-anther landing*: pollinators landed or hung directly on an M-anther and foraged or collected pollen from the M-anther without touching the stigma or L-anthers.
3. *L-anther landing*: syrphid flies hung on the L-anthers and ingested pollen from them directly (Fig. 2).

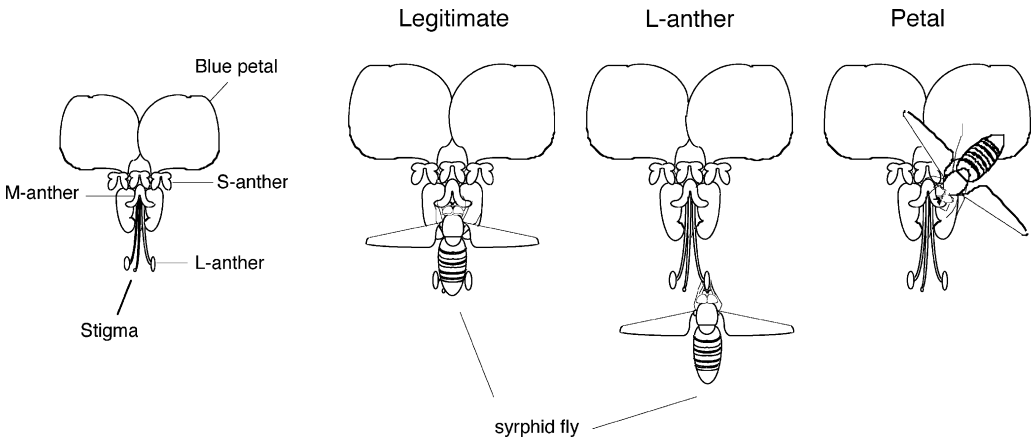


Fig. 2. *En face* views of *Commelina* flowers and landing types of syrphid flies.

4. *Petal landing*: pollinators foraged pollen from M- or S-anthers after landing on the blue petals (Fig. 2).
5. *Side landing*: pollinators landed on the bract or sepals at the side of the flower and fed on or collected pollen from the M-anthers without touching the stigma or L-anthers.

Syrphid flies exhibited all five types of landing, whereas M-anther and L-anther landings were not observed for bumblebees.

Analyses

For the analyses, we used the data from observations that included at least a single approach by a syrphid fly or bumblebee to an experimental flower. Approaches of syrphid flies to the experimental flowers were observed in all trials, while bumblebee approaches were seen in only 11 trials. Therefore, we used the data from 30 trials (70 Control, 53 Up and 57 Down flowers) to analyse syrphid fly behaviour and the data from 11 trials (24 Control, 23 Up and 20 Down flowers) for the bumblebee analyses.

We checked whether insects approached each selected flower. We also counted the number of respective landing behaviours on each flower type for each observation. Syrphid flies were often observed landing on a flower repeatedly (e.g. petal landing → legitimate landing → L-anther landing) in a single visitation bout; we counted this as one landing. When several landing types were observed in a single bout, we used their ratios to the total number of landings to quantify that behaviour. For example, if one legitimate landing and one petal landing were seen, we considered these as 0.5 and 0.5, respectively.

First, we compared the ratio of flowers to which at least a single insect approach was observed to the total number of flowers for Control and other flower types using the chi-squared test. This analysis applied a sequential Bonferroni test at a species-wide significance level of 0.05 (Rice, 1989). This analysis examined whether flower orientation affects the ability of pollinators to find flowers. Second, we compared the average number of total landings (per flower per 15 min) for each trial among treatments for both insect groups.

Then, we compared the average number of the respective landing types for each trial among treatments. One-way analysis of variance and the Tukey-Kramer procedure were used for these tests.

RESULTS

Natural flower orientation

At Ohara and Yamanaka, the flower angle ranged from 0 to 23° and from –17 to 29°, with means (± standard deviation) of 9.9 ± 6.1° and 6.3 ± 7.9°, respectively.

Field experiment

The ratio of approached flowers to the total number of flowers tended to be higher for Control (0.73 and 0.67 for syrphid flies and bumblebees, respectively) than the other flower types (Up = 0.58 and Down = 0.62 for syrphid flies, and Up = 0.57 and Down = 0.65 for bumblebees) for both insect types. However, the difference was not statistically significant (Control *vs* Up, $\chi^2 = 3.14$, d.f. = 1, $P = 0.07$ and Control *vs* Down, $\chi^2 = 1.56$, d.f. = 1, $P = 0.21$ for syrphid flies; Control *vs* Up, $\chi^2 = 0.51$, d.f. = 1, $P = 0.47$ and Control *vs* Down, $\chi^2 = 0.01$, d.f. = 1, $P = 0.91$ for bumblebees) (Table 1).

Down flowers tended to receive fewer syrphid fly and bumblebee landings than did Control flowers (Table 1). The analyses of variance revealed significant differences in the total number of landings among treatments for syrphid flies ($F = 7.38$, d.f. = 78, $P < 0.001$) but not for bumblebees ($F = 1.86$, d.f. = 29, $P = 0.17$). There were small differences in the total number of landings between Control and Up flowers for both insect groups (Table 1).

For both pollinator types, the mean number of legitimate landings was significantly higher for Control flowers than for the other flower types ($F = 16.9$, d.f. = 78, $P < 0.001$ and

Table 1. Mean number (± standard deviation) of landing types of syrphid flies and bumblebees for each experimental treatment

		No. of landings (/flower/15 min)					
Flower type	No. of trials	Total landings	Legitimate	M-anther	L-anther	Petal	Side
Syrphid fly							
Control	30	1.04 ± 0.76^{a}	0.51 ± 0.53^{a}	0.03 ± 0.11^{a}	0.39 ± 0.42^{a}	0.05 ± 0.17^{a}	$0.05 \pm 0.16^{a,b}$
Up	27	0.78 ± 1.12^{a}	0.09 ± 0.19^{b}	0.00^{a}	$0.22 \pm 0.32^{a,b}$	0.34 ± 0.71^{b}	0.15 ± 0.27^{a}
Down	24	0.19 ± 0.39^{b}	0.02 ± 0.10^{b}	0.04 ± 0.12^{a}	0.04 ± 0.14^{b}	$0.08 \pm 0.19^{a,b}$	0.00^{b}
Bumblebee							
Control	11	0.74 ± 0.72^{a}	0.74 ± 0.72^{a}	—	—	0.00^{a}	0.00^{a}
Up	11	0.44 ± 0.42^{a}	0.17 ± 0.24^{b}	—	—	0.14 ± 0.32^{a}	0.14 ± 0.23^{a}
Down	10	0.30 ± 0.42^{a}	$0.25 \pm 0.43^{a,b}$	—	—	0.00^{a}	0.05 ± 0.16^{a}

Note: The mean values with the same letter are not significantly different at $P = 0.05$ for each landing type for each insect group.

$F = 4.19$, d.f. = 29, $P < 0.05$; Table 1). No significant difference in M-anther landings by syrphid flies was found among treatments ($F = 1.42$, d.f. = 78, $P = 0.25$; Table 1). L-anther landings decreased significantly on Down flowers compared with Controls ($F = 7.69$, d.f. = 78, $P < 0.01$; Table 1). We observed significantly more petal and side landings on Up flowers than on the other flower types for syrphid flies ($F = 3.71$, d.f. = 78, $P = 0.029$ and $F = 3.98$, d.f. = 78, $P = 0.023$; Table 1). Down flowers received no side landings by syrphid flies (Table 1). Although the analyses of variance revealed no significant difference in the number of bumblebee petal and side landings, Up flowers tended to receive more petal landings than did other flower types ($F = 1.86$, d.f. = 29, $P > 0.05$ and $F = 1.97$, d.f. = 29, $P > 0.05$, respecitively).

DISCUSSION

The mean flower angle of *C. communis* was less than 10°, indicating that the flowers were nearly vertical, like other zygomorphic flowers (Neal *et al.*, 1998; Giurfa *et al.*, 1999). Syrphid flies and bumblebees always approached the *Commelina* flowers from the front (A. Ushimaru, personal observation), concordant with the idea that vertical presentation in zygomorphic flowers limits the approach of the pollinator to a flower (Neal *et al.*, 1998). For both syrphid flies and bumblebees, the ratio of approached flowers to the total number of flowers was slightly lower for Up and Down flowers than Control ones, and the difference between Control and Up flowers for syrphid flies was marginally statistically significant. The pollinators search for *C. communis* flowers using only the blue petals as floral cues (A. Ushimaru, T. Watanabe and K. Nakata, unpublished data). Because *C. communis* has a small side advertisement – a low ratio of the area of the side view to that of the *en face* view of the tepals (Dafni, 1994) – the flower-orientation changes affect the advertisement area from a certain angle. Our results suggest that such changes in the advertisement area of blue petals did not strongly influence pollinator attraction in this species. Perhaps this is because leaves and bracts often surround *C. communis* flowers, and thus the advertisement area has little effect on the ability of pollinators to find flowers. Otherwise, small sampling size may be responsible for the non-statistically significant difference in the ratio between Controls and other flower types. In heliotropic flowers, experimental changes in flower orientation significantly decreased pollinator attraction (Patino *et al.*, 2002; see also Kudo, 1995), which is inconsistent with our results.

Down flowers received fewer landings by both syrphid flies and bumblebees than did Control and Up flowers, which was consistent with our expectations. However, the difference for bumblebees was not statistically significant. In particular, syrphid flies rarely landed on Down flowers. There are two possible explanations for this.

First, the yellow anthers of *C. communis* function as pollen signals that can trigger pollen assessment behaviour and subsequent landing by pollinators (A. Ushimaru, T. Watanabe and K. Nakata, unpublished data; see also Lunau, 2000). In Down flowers, this signalling function may be weakened because the blue petals tended to obstruct the view of the yellow anthers for insects hovering in front of the flowers. Zygomorphic flowers have more complex floral patterns than do actinomorphic flowers (Neal *et al.*, 1998), and a change in *en face* orientation affects the presentation of these patterns, which might decrease flower attractiveness for pollinators. Furthermore, the downward orientation made the yellow anthers less accessible to pollinators physically than the other flower types because the blue petals reduced the freedom of approach to the yellow anthers. This would decrease the opportunity of

pollinators to assess pollen availability. Therefore, downward flower orientation might visually and physically diminish the function of the yellow anthers as pollen signals.

Second, footholds are limited in Down flowers. The most frequent landings on Down flowers by syrphid flies were landings on the back of the blue petals, while legitimate and L-anther landings, which were most frequently seen with Controls, were rare. We sometimes observed syrphid flies trying to hold onto M-anthers in Down flowers; however, most of these attempts were unsuccessful. These facts suggest that downward flower orientation makes it difficult for syrphid flies to land on the front of the flowers. By contrast, bumblebees could hang on to Down flowers, and most landings were legitimate. Bumblebees sometimes specialize in downward-oriented flowers (e.g. Kobayashi *et al.*, 1997; Huang *et al.*, 2002; Mahoro, 2003), thus downward orientation does not appear to limit footholds for bumblebee landings. Although we did not measure the handling time of bumblebees, they appeared to take longer to land on Down flowers than on Controls. Tadey and Aizen (2001) suspected that the down-facing orientation of hummingbird-pollinated flowers increases the handling time of pollinators, resulting in greater stigmatic pollen deposition. Therefore, increased handling time may enhance pollination success, although this also decreases the foraging efficiency of pollinators, which sometimes results in discrimination against the flowers (Waser and Price, 1983, 1985). In fact, we observed bumblebee landings on Down flowers early in our experiments but not during the later stages, although we did not consider the effect of learning by bumblebees in this study. We should distinguish the difference in the reaction to experimental flowers between naive and experienced pollinators in a future study.

Our results show that the change to a downward orientation affected pollinator behaviour differentially, depending on insect species. This difference may come from the difference in physical leg strength between insect groups. Nevertheless, the decrease in the number of landings with downward flower orientation must decrease the chance of insect-mediated pollen transfer in *C. communis*.

For both insect groups, the total number of landings did not differ significantly between Control and Up flowers. However, legitimate landings were seen more frequently with Controls than with Up flowers, while petal (and side) landings increased with Up flowers. More than half of the total landings on Up flowers by both insect groups were petal and side landings. These findings are also concordant with our expectations. In Controls, both syrphid flies and bumblebees rarely used blue petals, perhaps due to their vertical structure. An upward orientation made blue petals function as a horizontal landing site, giving syrphid flies and bumblebees easy access to the M-anther pollen from the petals, which increased pollen-thieving behaviour. These observations indicate that the chance of insect-mediated pollen transfer also diminishes with upward flower orientation in *C. communis*.

In summary, our experimental results show that downward and upward orientations decreased the numbers of total landings and legitimate landings, respectively. This may subsequently reduce outcross pollination success, although this was not assessed. Many studies have revealed that flower orientation influences pollinator attraction (Hocking and Sharplin, 1965; Kevan, 1975; Kudo, 1995; Patino *et al.*, 2002). To our knowledge, this is the first experimental study to show that floral orientation affects pollinator behaviour after arriving at plants in angiosperms and we believe that our idea could apply to other zygomorphic taxa such as Orchidaceae, Fabaceae and so on. To generalize our findings, we need to examine the effect of flower orientation on pollinator behaviour in other zygomorphic and actinomorphic flowers of many plant taxa.

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