



Original article

Effect of change in floral openness with floral age on floral display and reproduction in *Gentiana*

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ABSTRACT

Some plant species have flowers that open widely and then close slowly over time, resulting in changes in the width of the corolla opening. We examined the adaptive significance of retaining flowers with relatively closed corollas using *Gentiana triflora* var. *japonica*, a perennial species with petal movement, in Hakkoda, northern Japan. Under open pollination, floral openness changed with floral age. It increased from days 1–3 after the flower initially opened and decreased thereafter until floral senescence. Hand-pollinated flowers showed a significant reduction in floral openness compared with unpollinated flowers, suggesting that a floral openness reflects its demand for pollination. Pollinators visited inflorescences with many flowers irrespective of their openness, suggesting that the reduction in floral openness does not affect the attractiveness of the inflorescences to pollinators. Within inflorescences, pollinators visited less-pollinated flowers with wider floral openness more frequently and more-pollinated flowers with lower floral openness less frequently, possibly because of the time cost of entering flowers with low openness. This strategy appears adaptive because if all flowers maintain wide floral openness irrespective of their pollination demand, pollinators may visit more-pollinated flowers in an inflorescence and may leave the inflorescence without visiting less-pollinated flowers. Reduction of openness of more-pollinated flowers fits a strategy of enhancing effective pollination within inflorescences.

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1. Introduction

The size of floral displays plays an important role in the reproductive success of animal-pollinated plants by affecting the attractiveness of plants to pollinators (Vaughton and Ramsey, 1998). In general, inflorescences with relatively large displays are frequently visited by pollinators. This could result in an increase in outcrossing, and thus large displays may be advantageous for plants (Ohashi and Yahara, 2001). In this case, natural selection may favor the simultaneous opening of flowers, as well as the maintenance of old flowers. On the other hand, large displays could result in an increase in geitonogamous pollination (de Jong et al., 1993; Snow et al., 1996) because pollinators tend to increase successive probes within inflorescences with large display sizes (Geber, 1985; Klinkhamer et al., 1989; Robertson, 1992; Harder and Barrett, 1995). Furthermore, keeping displays large by maintaining old flowers is costly (Ashman and Schoen, 1994) and may result in fewer visits to

unpollinated flowers, considering that pollinators do not, in general, visit all open flowers within an inflorescence (Jordan and Harder, 2006; Ishii et al., 2008). One alternative strategy seen in flowering plants, which keeps the floral display large but directs pollinators to newly open flowers that need to disperse and receive pollen, is change in floral color with floral age (Gori, 1983). Color-changed older flowers contribute to pollinator attraction from a distance, and within inflorescences, pollinators can discriminate new flowers from old ones (Casper and La Pine, 1984; Gori, 1989; Weiss, 1991; Niesenbaum et al., 1999; Oberrath and Bohning-Gaese, 1999).

A similar phenomenon in some species is daily petal movement, in the form of daily opening and closing of flowers (Costeloe, 1988; Petanidou et al., 1995a, 1995b, 1995c; Kozuharova and Anchev, 2001, 2002, 2004). There are 1000 to 3500 such species (Simons, 1992; von Hase et al., 2005), occurring in 156 genera belonging to 17 different plant families (Stirton, 1983; Struck, 1994; Goldblatt et al., 1995; Smith et al., 1998). In these species, floral openness can be variable, from complete closing to full opening, so that floral display size also changes and is associated with the changes in

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floral openness of individual flowers. Then, if the floral openness changes with its demand for pollination, with less-pollinated flowers showing wider openness, and if pollinators frequently visit flowers with wide openness, plants may be able to direct pollinator visits. Therefore, less-pollinated flowers are visited more frequently and more-pollinated ones less frequently. Thus, changes in floral openness may be a strategy to enhance the efficient pollination of young flowers within inflorescences, possibly at the expense of pollinator attraction to the inflorescence. However, it is also possible that flower closure evolved for the protection of flowers from snow, hail, rain, cold temperature, high light intensity, and from microorganisms (van Doorn and van Meeteren, 2003).

Gentiana triflora Pall. var. *japonica* (Kusn.) H. Hara is a plant with petal movement, with its petals opening in the morning and closing in the afternoon. *Gentiana algida*, *Gentiana leucomelaena*, and *Gentiana straminea*, related species, also shows daily opening and closing in response to ambient temperature (Bynum and Smith, 2001; He et al., 2006; Mu et al., 2010). In *G. triflora* var. *japonica*, temperature also seems to be one of the factors affecting petal movement because its flowers often remain closed if the air is cold, even on clear days. However, other factors may affect petal movement because there is variation in openness among flowers in the same inflorescences.

In this study, using *G. triflora* var. *japonica*, we investigated how the floral openness of individual flowers in a plant affects its reproductive success. Therefore, we experimentally investigated the following questions. 1) What kind of pollinator behavior is affected by floral openness? 2) Does hand pollination influence floral openness?

2. Materials and methods

2.1. Study sites and study species

We studied *G. triflora* var. *japonica* naturally growing in the Botanical Laboratory of Tohoku University (40°42'N, 140°55'E, 890 m a.s.l.) located on Mt. Hakkoda, Aomori Prefecture, northern Honshu, Japan.

G. triflora var. *japonica* is a self-compatible herbaceous perennial that grows in marshlands and mountain lands in northern Japan. This species makes genets each composed of 4.8 ramets on average, and each flowering ramet produces 1–15 blue flowers from September to early October. Hereafter, we refer to all of the flowers of a ramet as an inflorescence. Approximately 1–8 flowers open simultaneously in each inflorescence. Flowers are incompletely protandrous, and anthers dehisce before pistil elongation and the unfolding of stigmatic lobes with a slight overlap between the two sexual phases (Kato and Sakai, 2008). Flower longevity ranges from 3 to 9 days, and the mean days from flower opening to the stigmatic lobes becoming unfolded, and from the stigmatic lobes unfolding to the end of flowering, are 1.7 and 3.9, respectively. Flowers start with anthers being dehisced and corollas being closed. Then corollas open up to maximum opening, and gradually close with floral age. Here, during flowering period, corollas may close to various degrees including partial to complete closure and re-open again. Corollas finally close at the end of floral longevity. During flowering period, pollinators can enter completely closed flowers, but it seems to be difficult to enter pre-opened flowers because the corollas of those flowers are tightly closed. Kato and Sakai (2008) reported that nectar volume of a flower decreased with floral age in this species. The main pollinator is the bumblebee *Bombus diversus diversus*. Horseflies sometimes approach *Gentiana* flowers, but they are not effective pollinators because they do not actively enter flowers.

2.2. Floral openness

In all of the experiments, we recorded observed floral openness (from 0 to 4) as follows: openness 0 (diameter of open area was 0 mm), openness 1 (that was 0 mm < ≤3 mm), openness 2 (that was 3 mm < ≤8 mm), openness 3 (that was 8 mm < ≤15 mm), and openness 4 (that was 15 mm <). Pollinators can enter flowers with openness 0 even though these flowers are completely closed.

To examine the overall tendency in the changes in floral openness with floral age (days from flower opening), we observed floral openness of 937 flowers throughout the flowering season in 2011. We calculated the mean floral openness of flowers for each age, including flowers of all positions in inflorescences.

2.3. What kind of pollinator behavior is affected by floral openness?

In 2011, pollinators were observed with HDD video cameras (Sony Handycam DCR-SR100 and Sony Handycam HDR-XR150, Tokyo, Japan), from 10:00 to 12:00 h for 8 days between 7 and 27 September. Approximately six inflorescences were observed every census day. Before observation, we counted the flowers in each inflorescence, recorded the openness, the flowering date, the flower age, and the flowering order of each flower. The height of each inflorescence was calculated as the height of the flower intermediate between the lowest and the highest flowers. After observation, we recorded the maximum floral openness of each flower during the video recording, the number of visits to each inflorescence, the number of pollinators entering each flower within the inflorescence, the number of rejections by pollinators after they approached a flower, and the sequence of flowers probed on an inflorescence. We also recorded the durations of entering, staying inside, and exiting, to 0.1 s for each pollinator visit to a flower. We defined the duration of entry into a flower as the time between when a pollinator first touched a petal and when it stopped its movement to collect nectar; the duration of stay inside a flower as the time inside of the flower without movement; and the duration of exit from a flower as the time between the beginning of movement to leave and actual exit from a flower. We also calculated the mean length of flowers (length from the top of the petals to the base of the sepals) in the inflorescence flowering on that day.

In the statistical analyses, we evaluated the effects of floral openness on the following four behaviors of pollinators: visitation to inflorescences, flower selection within inflorescences, successive visits to flowers within the inflorescence, and durations of entering a flower, staying inside a flower, and exiting a flower.

Random forests (RF) (Breiman, 2001) were used for these analyses except for the flower selection. RF is a machine-learning algorithm that combines thousands of decision trees to identify the relationships between response and explanatory variables. RF can also calculate a measure of relative importance of explanatory variables. Although RF originated in the field of machine learning, it sometimes outperforms other conventional statistical methods in the analysis of ecological data (Cutler et al., 2007). Models were fitted using the *cforest* function in the *party* package (Cutler et al., 2007; Strobl et al., 2007, 2008) in R, considering the original algorithm for the calculation of an importance measure is biased by correlations among explanatory variable (Strobl et al., 2009). We then constructed 30,000 decision trees for fitting each model. In the analysis of visitation to inflorescences, the total number of visits to an inflorescence (including both visits in which pollinators entered some flowers and those in which they entered no flower after approaching) was a response variable, and the observation date, inflorescence height, mean length of flowers in the inflorescence, and numbers of the flowers in one of the five openness classes, ≥0,

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