

Commentary

When plants get bent out of shape: a new twist in plant reproduction

For more than 150 years, evolutionary biologists have spent much of their time – in the words of Jerry Coyne (1994) – ‘sweeping up behind the Darwinian elephant’, exploring and expanding upon the droppings from his groundbreaking and extensive writings. This argument can easily be extended to plant reproductive biology and sensory systems where current literature often builds upon topics in Darwin’s almost incomprehensively broad body of work: plant mating systems, inbreeding depression, plant–pollinator interactions, plant responses to light and gravity, and movement in vines and carnivorous plants to name a few (e.g. Darwin, 1862, 1877, 1880). Yet in this issue of *New Phytologist*, Armbruster & Muchhala (2020; pp. 232–243) explore a plant phenomenon that apparently went unnoticed or at least undocumented by Darwin and other early giants of floral biology. Combining observation, simple experimental manipulations, and quantitative analysis, they show that plants can recover from damage by readjusting the orientation of their flowers to optimize pollinator attraction and effectiveness. The study emerged from keen observations of plants in the natural environments and it introduces a new area of investigation that spans major disciplines in plant biology.

‘The discovery of floral reorientation after accidental damage underscores the value not only of observing organisms carefully, but of making those observations in natural field settings . . .’

A hazard of being a plant is the inability to dodge a falling limb or animal’s footfall or to hunker down in a strong wind. As a result, plants often experience accidents that bend or knock over a stem. If vascular tissue remains intact, the structure may continue to be viable. But if flowers are involved, the resulting change in orientation can affect their functioning by reducing attractiveness or disrupting the proper placement of pollen on the body of a pollinator. Armbruster & Muchhala report that some plants have

mechanisms to salvage the function of flowers in the face of such damage. In a phylogenetically and geographically widespread sample, plant species responded in varying degrees to naturally occurring accidents or experimentally manipulated inflorescences by restoring proper floral orientation. Drawing on models developed in their work on floral adaptation and specialization, Armbruster & Muchhala use detailed measurements to quantify this correction in terms of adaptive inaccuracy, or a deviation from the optimal phenotype for effective pollen transfer.

When a normally upright stem is placed on its side, it will bend to grow again in the upright direction in a response to gravity mediated by auxin gradients. Could the observed restoration of floral orientation simply be part of this broader gravitropic response? Armbruster & Muchhala suggest that the ability to reorient skewed flowers is an adaptation shaped specifically by the selective effects of pollinator visitation and effectiveness. As support for their hypothesis, they test a prediction based on the following logic: radially symmetrical flowers can be approached by pollinators from multiple directions with equal effectiveness, whereas bilaterally symmetrical flowers are usually approached from a single direction, resulting in precise placement and transfer of pollen. As a result, species with bilaterally symmetrical flowers should experience stronger selection on flower orientation. If reorientation after damage is an adaptation driven by pollinator interactions, it should evolve most readily in those species. Comparing species of the two floral types, Armbruster & Muchhala find support for their hypothesis: on average, species with bilaterally symmetrical flowers showed greater ability to restore original floral orientation than did those with radial symmetry.

Organisms do not always fit neatly into simple categories, though, and observing the complicated details of real world biology can provide further insights. While the two forms of floral symmetry are a familiar feature of dichotomous botanical keys, the actual diversity of flower structural plans is more complex. Armbruster & Muchhala document floral reorientation in a species that has bilaterally symmetrical petals but radially symmetrical sex organs. They argue that, since floral misorientation should not affect relative position of stigma and anthers or pollen placement on a pollinator, evolution of the corrective mechanism in this case must be driven solely by pollinator attraction. Remarkably, in a species showing the reverse arrangement – radially symmetrical petals and bilaterally symmetrical stigma and anther position – the response to mishaps is accomplished by a turn of the stamens, ensuring proper placement of pollen without any change in whole flower orientation.

While Armbruster & Muchhala provide new evidence for floral reorientation as a response to damage, developmental changes in the position of flowers is well described, primarily in the Orchidaceae. Floral buds of most orchid species undergo torsion to place the ornamented petal (labellum) that often acts as a landing

This article is a Commentary on Armbruster & Muchhala (2020), 227: 232–243.

platform for pollinators at the lowermost position on a mature flower – a process termed resupination. While this torsion is a standard developmental feature of orchid species, it also appears to be flexible in response to gravity cues. Nyman *et al.* (1984) showed that buds on orchid stems held at an angle modify the extent of twisting to achieve the same final floral orientation as those on upright stems. Armbruster & Muchhala's findings suggest that similar adjustments can occur in a wider taxonomic array of species, at later developmental stages, and can serve an essential function in coping with accidents.

Armbruster & Muchhala's study raises interesting questions and suggests further avenues to explore. They point out that, since the reorientation of flowers takes time to occur, its benefits would be greatest in relatively long-lived flowers. Is the phenomenon absent in species with ephemeral flowers? We might also predict that the response would be lost in species that are self-fertilizing, perhaps adding to a suite of floral traits, such as small petals and low pollen production that arise in concert with the evolution of selfing. Indeed, self-fertilization is common in orchid species that do not undergo resupination (Rudall & Bateman, 2002). How often has floral reorientation evolved? Armbruster & Muchhala find that the process occurs in different ways in different species, variously involving the turn of an entire inflorescence, the twist of an individual flower, or even a stamen. This diversity of mechanisms suggests multiple parallel origins, and broader sampling might reveal insights into the ecological conditions or pollinator assemblages in which it is most beneficial.

More broadly, the reorientation response documented by Armbruster & Muchhala inspires further exploration of the interface between pollination biology and plant sensory systems, two areas that have long captured the interest of plant biologists. Flowering plants exhibit diverse and clever mechanisms to promote the efficient fertilization of flowers by animals. For example, in species with heterostyly – a reproductive system in which multiple floral morphs show reciprocal differences in the height of anthers and styles – pollen is placed onto a pollinator by one morph in a position that optimizes delivery to the stigma of another. Another branch of science has documented the astounding abilities of plants to respond to light, gravity, chemicals, touch, and sound, even inspiring debate on the concept of plant intelligence (e.g. Trewavas, 2003; Firn, 2004). Armbruster & Muchhala report a new role for plant sensory response in the pollination of flowers. Other examples of this integration come to mind. In plants of several families, two-lobed stigmas close when touched by a pollinator, a mechanism that has been shown to increase pollen export (Fetscher *et al.*, 2002). Pollen of *Campanula* is presented to pollinators during a flower's male phase on stylar hairs. When pollen is removed, flowers transition more rapidly to a female phase where the stigma becomes receptive (Evanhoe & Galloway, 2002). And in a well-known example, young sunflowers track the sun's position in a process regulated by circadian rhythms entrained by light and, when mature, direct their flowering heads eastward to maximize pollination visitation (Atamian *et al.*, 2016). What additional mechanisms will be uncovered as these two vibrant fields in plant science are further integrated?

As Armbruster & Muchhala's study reminds us, progress is likely to require keen inspection and attention to natural history. Indeed,

centuries after the detailed observations of Darwin, Sprengel, and others built the foundation of conceptual understanding of plant reproduction, novel phenomena are still being described. In a new twist on resupination, Harley *et al.* (2017) recently discovered an unusual dimorphism in *Eplingiella*, a shrub in the mint family: in one morph, plants display their bilaterally symmetric flowers in an upright direction, while in the other, a turn of the pedicel orients flowers upside down, promoting cross-pollination between morphs. What is learned by studying and describing organisms can launch new research arenas (Greene, 2005). The discovery of floral reorientation after accidental damage underscores the value not only of observing organisms carefully, but of making those observations in natural field settings where organisms are challenged to respond to the variation and unpredictability of the dynamic environments they inhabit.

ORCID

Carol Goodwillie  <https://orcid.org/0000-0003-2649-2771>

Carol Goodwillie 

Department of Biology, East Carolina University, Greenville,
NC 27858, USA
(tel +1 252 328 4225; email GOODWILLIEC@ecu.edu)

References

- Armbruster WS, Muchhala N. 2020. Floral reorientation: the restoration of pollination accuracy after accidents. *New Phytologist* 227: 232–243.
- Atamian HS, Creux NM, Brown EA, Garner AG, Blackman BK, Harmer SL. 2016. Circadian regulation of sunflower heliotropism, floral orientation, and pollinator visits. *Science* 353: 587–590.
- Coyne JA. 1994. Ernst Mayr and the origin of species. *Evolution* 48: 19–30.
- Darwin CR. 1862. *On the various contrivances by which British and foreign orchids are fertilised by insects*. London, UK: John Murray.
- Darwin CR. 1877. *The different forms of flowers on plants of the same species*. London, UK: John Murray.
- Darwin CR. 1880. *The power of movement in plants*. London, UK: John Murray.
- Evanhoe L, Galloway LF. 2002. Floral longevity in *Campanula americana* (Campanulaceae): a comparison of morphological and functional gender phases. *American Journal of Botany* 89: 587–591.
- Fetscher EA, Rupert SM, Kohn JR. 2002. Hummingbird foraging position is altered by the touch-sensitive stigma of bush monkeyflower. *Oecologia* 133: 551–558.
- Firn R. 2004. Plant intelligence: an alternative point of view. *Annals of Botany* 93: 345–351.
- Greene HW. 2005. Organisms in nature as a central focus for biology. *Trends in Ecology and Evolution* 20: 23–27.
- Harley RM, Giuletti AM, Abreu IS, Bitencourt C, di Oliviera FF, Endress PK. 2017. Resupinate dimorphy, a novel pollination strategy in two-lipped flowers of *Eplingiella* (Lamiaceae). *Acta Botanica Brasiliica* 31: 102–107.
- Nyman LP, Soediono N, Arditti J. 1984. Opening and resupination in buds and flowers of *Dendrobium* (Orchidaceae) hybrids. *Botanical Gazette* 145: 215–221.
- Rudall PJ, Bateman RM. 2002. Roles of synorganisation, zygomorphy and heterotopy in floral evolution: the gynostemium and labellum of orchids and other lilioid monocots. *Biological Reviews* 77: 403–441.
- Trewavas A. 2003. Aspects of plant intelligence. *Annals of Botany* 92: 1–20.

Key words: floral orientation, gravitropism, natural history, plant sensory system, pollination, resupination.