

RECENT ADVANCES IN BOTANICAL DARWINIAN TOPICS: HETEROSTYLY, LIANAS AND TRADE-OFFS

This issue of *Botanical Sciences* includes three papers related to topics that were important to Charles Darwin: the evolution of heterostyly (Sosenski *et al.*, 2015), climbing plants (Ibarra-Manríquez *et al.*, 2015; the diversity of lianas in Mexico) and trade-offs (Torres-García *et al.*, 2015; implicated in the evolution of herbicide resistance in an important weed).

Sosenski, Fornoni and Domínguez (2015) explore through a statistical meta-analysis the available information regarding the evolution of heterostyly—in particular tristyly—accumulated since Charles Darwin's pioneer book (1877). Darwin was fascinated by this group of mysterious plants: heterostylic species have two (dystylic) or three (tristylic) reproductive morphs; each morph is hermaphroditic, with perfect flowers, but they display reciprocal differences in the length of the style and the anthers, as shown in the classic original figure of Darwin's book (1877) (Figure 1). Each morph is usually self- and within morph-sterile (they need pollen from another morph to produce seeds); thus in practice they have a complicated sexual system, with different “sexes”, but each one hermaphroditic. How these complex polymorphisms evolved and are maintained remains a mystery, even today. However, recent information on their ecology, efficiency in the movement of pollen, inbreeding depression, genetics, and in particular the proportion of flowers per morph, is discussed and analyzed in Sosenski *et al.* (2015), and will eventually help us to answer these questions.

Tristyly plant species have independently evolved several times within the angiosperms, including species from two monocot (Pontederiaceae and Amaryllidaceae), and five dicot families (Lythraceae, Oxalidaceae, Connaraceae, Linaceae and Thymelaeaceae). Sosenski *et al.* (2015) re-analyze data from ten tristyly species—although adequate data were available only for five—for a total of 541 populations (391 tristyly, 93 distyly (populations that have lost one morph) and 42 monomorphic (that lost two of the morphs). It is expected that all morphs should be in the same frequency (“isoplectic” proportions), an evolutionary stable state (Heuch, 1980). Surprisingly, they found that most populations are not isoplectic, but instead one morph is more frequent.

In some species, like *Lythrum salicaria*, *Narcissus triandrus* and *Oxalis alpina*, the most common morph is the long one, while in *Pontederia cordata* is the short one; in most cases, but not always, the intermediate morph is the rarest. All the studied species show a substantial proportion of populations with only two morphs, and three species have monomorphic populations. In one case, (*Decodon verticillatus*) 33 % of the populations are monomorphic.

These results represent an interesting paradox, another abominable mystery for Darwin: If ecological data suggest that tristyly is unstable, how is this polymorphism

maintained? Why has it evolved in at least seven independent lineages within the angiosperms?

As discussed by Sosenski *et al.* (2015) fine and detailed studies to estimate the paternal (pollen) component of fitness will aid to solve the puzzle. Today we can complement these studies with field experiments and with the use of molecular markers and genomic information, obtain the phylogeny of each group and perform comparative method analyses to disentangle the genetic basis of these floral polymorphisms. This will help to finally solve this Darwinian mystery in the near future.

Darwin was also fascinated with climbing plants (1865, 1867). He suggested that the main adaptation of climbing plants consisted in how they resolved a major tradeoff problem that evolved in very different groups of plants, indicating convergent evolution: “Plants become climbers, in order, it may be presumed, to reach the light, and to expose a large surface of leaves to its action and to that of the free air. This is effected by climbers with wonderfully little expenditure of organized matter, in comparison with trees, which have to support a load of heavy branches by a massive trunk. Hence, no doubt, it arises that there are in all quarters of the world so many climbing plants belonging to so many different orders.” (Darwin, 1865, pages 107-108). Again, we have a common adaptation that has evolved in an independent way in several plant lineages, and its advantage is clearly the result of solving a mechanical tradeoff: if you do not need to spend in wood and support, you can efficiently use this energy to grow and reproduce.

In particular, lianas are woody climbing vines that are an important component of tropical forest; in fact, the abundance of lianas is a distinctive attribute of tropical rain forests (Richards, 1952), but they have been extremely difficult to study and assess their ecological relevance. In this issue of *Botanical Sciences*, Ibarra-Manríquez *et al.* (2015) describe for the first time the diversity and distribution of the lianas of Mexico.

According to Ibarra-Manríquez *et al.* (2015) a total of 133 families of plants are climbers, and their success represent a solution for the Darwinian tradeoff described above. Lianas can represent up to 25 % of the woody plant diversity in tropical dry forest, and a very high proportion of the total photosynthetic biomass. From nearly

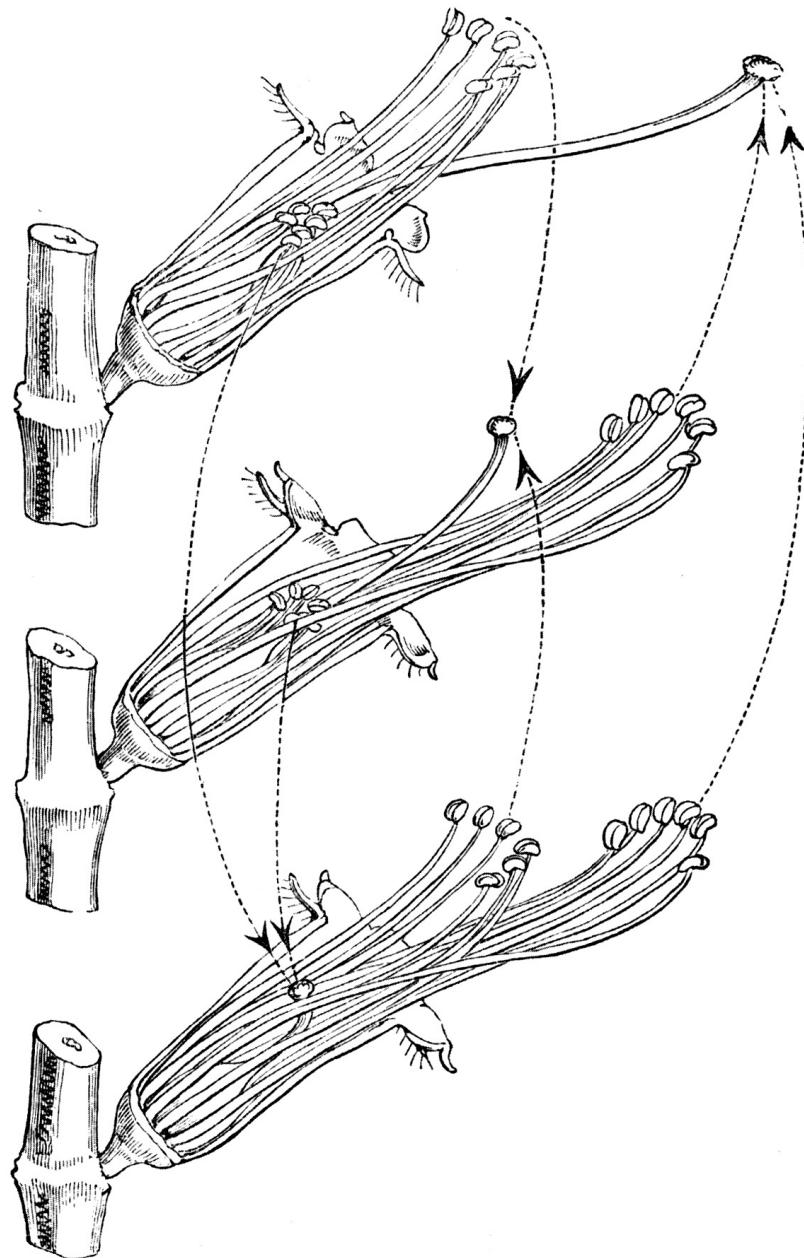


Figure 1. Darwin's (1877) classic diagram of the three floral morphs of the trystilous plant *Lythrum salicaria*. The corolla was removed and the arrows show the direction of the legitimate (fertile) pollinations. (Reproduced with permission of van Wyhe ed. 2002. The Complete Work of Charles Darwin Online <<http://darwin-online.org.uk/>>).

22,000 species of angiosperms in Mexico, Ibarra-Manríquez *et al.* (2015) documented 861 species of lianas, belonging to 250 genera and 59 families. A total of 25.9 % of these species and three genera are endemic to Mexico. At the family level, Apocynaceae and Fabaceae are the most important; while the genus *Ipomoea* (Convolvulaceae) has the highest number of liana species (43). In Mexico, the greatest diversity of lianas is found in Chiapas State, including 57 out of 59 plant families of lianas, 85.2 % of the genera, 65.4 % of the total species, and 20 % of the species exclusive to the State. The richest State in terms of endemisms is Oaxaca with 111 liana species. This study is a keystone contribution to Mexican botany, and without any doubt will aid conservation efforts and detailed ecological studies in the future.

We have already illustrated the importance of the tradeoff concept in Darwin's thought. Also, in this issue Torre-García *et al.* (2015) demonstrated an important tradeoff in the evolution of herbicide resistance in the grass *Phalaris minor*, an important weed in cultivated fields in the Bajío region, in Central Mexico. This grass has evolved resistance to herbicides of the lipid inhibitors class, specifically ACCase inhibitors. Selective pressure to evolve herbicide resistance can be extremely strong, since herbicides can kill up to 99.99 % of plants in a population. Using a collection of 20 populations of *P. minor* resistant to diclofop from the Bajío region, Torres-García *et al.* (2015) evaluated in detail physiological characters of seeds from four collections that had independently evolved resistance. Clear tradeoffs were found associated with herbicide resistance: the embryo of resistant accession was reduced up to 50 %, with an associated increase in the time required to germinate, and a reduction in germination speed. Also, the resistant accessions displayed membrane damage, and an overall lower seed vigor.

Thus, the study shows a clear cost and a tradeoff to herbicide resistance, illustrating the ideas recently developed by R. Ford Denison in his important book on Darwinian Agriculture (2012): there are important tradeoffs in many agriculture relevant traits in plants, both cultivated and weeds, and even if you can select or introduce (as for instance using transgenic methods) genes for resistance to a herbicide, it is very likely that other components of plant fitness will be reduced.

The implications of these ideas to crop management and for a rational biotechnology are critical and will be explored in a future contribution by the authors of this commentary.

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