

Partridge Berry: Simple Beauty Belies Complexity

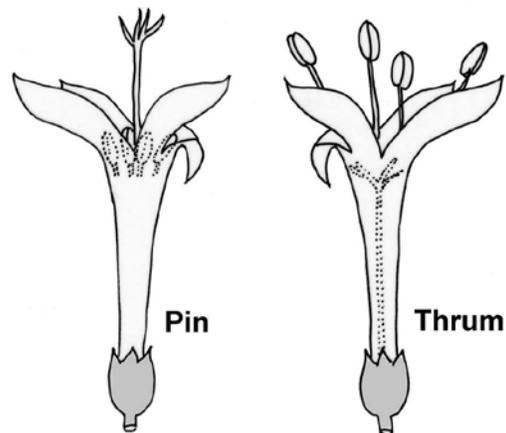
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Superficially, plants seem so simple. Rooted in place, they do not move around. And while plant growth is a dynamic process, without time-lapse photography, growth events are so imperceptibly slow that, to us impatient humans, plants seem both immobile and static. Nevertheless, there is a lot going on inside the plant body, and this is especially true for the events of reproduction that play out inside flowers and fruits. As one of my students recently commented, “I used to think it was just a matter of pollen plus stigma and, presto-change-o, seeds happen.” That student, I hope, learned otherwise, as will anyone else who takes the time to study the biology of flowers in detail.

Take, for example, the 2012 Wildflower of the Year, partridge berry (*Mitchella repens*). Flowers appear in late spring and continue somewhat sporadically through the summer. In any given patch of partridge berry, it is most likely that all the flowers will appear identical. But if one carefully examines flowers from multiple colonies, it will be apparent that this species produces two different flower forms (see figure). In other words, the flowers are heteromorphic. In some flowers, stigmas protrude beyond the corolla while anthers are hidden within the corolla tube. In other flowers, the pattern is reversed, stamens are long with protruding anthers and styles are short, with the stigmas hidden inside the corolla tube. This particular form of floral heteromorphism is known as distyly, a reference to the long and short styles, but it is important to remember that stamen length and, hence, anther position also vary in distylous flowers.

Some two dozen families of flowering plants have distylous flowers, and distyly is particularly common in Rubiaceae, the family in which *Mitchella* is classified. Other examples of plants with distylous flowers include primroses (*Primula*), flax (*Linum*), and loosestrife (*Lythrum*). (In fact, some loosestrife species have tristylous flowers, i.e., short, medium, and long forms of both styles and stamens.) By convention, long style flowers are called “pin” flowers, which is descriptive of flowers like primroses in which the stigma resembles a round-headed pin; long stamen/anther flowers are known as “thrums,” an obscure reference to the ragged ends of threads protruding from woven cloth. Despite the fact that the four flap-like stigmas of partridge berry in no way resemble pin-heads, for consistency with the



terminology applied to other species, long-style partridge berry flowers are still termed pins (see figure).

So, what is the point of distylous floral heteromorphy? As it turns out, the two different floral forms are part of a system of adaptations that control pollination, and hence, the subsequent fertilization of ovules that, in turn, impacts the genetic composition of the seeds produced. The way the system works is that pollen from long stamens with protruding anthers (thruns) functions only on flowers with long styles and protruding stigmas (pins); conversely, pollen from pin flowers can function only on thrum stigmas. Self-pollination fails, as does thrum pollen on stigmas of other thrum flowers, and pin pollen on stigmas of other pin flowers. Cross-pollination, of course, promotes genetic diversity among the seeds and seedlings that constitute the next generation, and genetic diversity within a population is generally considered beneficial for the ability of a population to adapt to ever-changing environmental conditions.

The essence of distyly is that, although all pollen and stigmas are functional, only pin and thrum combinations will succeed and all pin-to-pin and all thrum-to-thrum combinations are incompatible. Clearly, something beyond mere length of stamens and styles must be operating to control the success or failure of pollination in distylous flowers like partridge berry. As it turns out, there are genes governing self-incompatibility interactions at the cellular and molecular level that cause pollen tubes to abort, and these genes are tightly linked with the genes that control stamen and style length. The details of how self-incompatibility works varies from one group of plants to another, but regardless of the details, self-incompatibility genes are usually denoted by the symbol S .

In the most generalized example of how these systems work, the self-incompatibility gene has numerous alternative forms (alleles) designated as $S_1, S_2, S_3, \dots S_n$. These alleles are expressed by the production of certain proteins, both in the cells of the style and stigma and in the pollen grains. Because the floral heteromorphism genes are tightly linked to the incompatibility genes, pin-to-pin and thrum-to-thrum pollinations bring pollen grains into contact with style and stigma cells expressing exactly the same proteins. It is the interaction of identical proteins that results in the abortion of the pollen tube. However, if the genes present in stigmas/styles and pollen are completely different, as in pin-to-thrum combinations, no such interaction occurs, the pollen tube functions normally, and this cross-pollination results in a fertilization between genetically different gametes.

There are two basic variations in the generalized self-incompatibility system described above, distinguishable by the details of pollen genetics. In some cases, it is strictly the genetic constitution of the pollen cells that determines compatible/incompatible combinations; such systems are termed "gametophytic." In other cases, called "sporophytic incompatibility," it is the genetic constitution of the

diploid pollen parent that matters, even though the haploid pollen grains carry just one of the incompatibility alleles; this is because the pollen grain surface is built not just by the haploid cells of the pollen grain itself, but also by other diploid cells of the anther tapetum, so these pollen grains actually express two incompatibility alleles. Still, the basic principles of incompatibility apply, only unique combinations of alleles result in successful pollination events.

The form of self-incompatibility found in partridge berry is of the sporophytic type as described above, but in combination with floral heteromorphism (distyly), there are a few additional complications. In all cases for which the underlying genetics for distylous self-incompatibility are known, there are just two self-incompatibility alleles, S and s, and all individuals in a population are either Ss or ss. Further, the S allele is dominant over s. Successful pollination (and subsequent fertilization) is possible only in Ss X ss crosses; even though such crosses share the s allele from both parents, the effect of the S allele dominates so these crosses are effective. As in any self-incompatibility system, self-pollinations or crosses involving the same genotypes (ss X ss or Ss X Ss) fail. In theory, because the incompatibility alleles are tightly linked to the genes controlling style and stamen length, distylous sporophytic incompatibility mechanisms should result in a nearly 1:1 ratio of pin populations to thrum populations. Tallies of floral form in natural populations support the predicted 1:1 ratio, not just for partridge berry, but for other distylous species as well.

Next time you stumble upon partridge berry while rambling through the woods, pause for a moment to ponder how these seemingly simple, dainty, jewel-like plants engage an intricate reproductive system to control compatible pollinations and maintain robust, genetically diverse, populations. Simple plants? Hardly!

--W. John Hayden, VNPS Botany Chair

Sources

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