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Bloodroot Pollination: Bet-Hedging in Uncertain Times

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Bloodroot reproduction plan:
Hurry up and wait, and then hedge your bets

"Hurry up and wait." The phrase that epitomizes life in the military or any other large, bureaucratic, organization, applies surprisingly well to bloodroot and similar ephemeral wildflowers. Each year these plants race to flower as early as possible to assure sufficient time for fruits to ripen and seeds to mature while sunshine is abundant at the forest floor, for all too soon the forest floor will be draped in shadows cast by the trees' leafy canopy. Ephemerals do everything quickly: sprout, grow, flower, disperse seeds, and re-enter dormancy.

But flowering in very early spring can be risky. Some days will be fair and pleasant, but just as surely other days will be cool and drizzly, making successful pollination by insect visitors uncertain. In general terms, plant ecologists have proposed that self-pollination (autogamy) should be common in plants that bloom under unpredictably variable conditions. In fact, some ecological studies have concluded that bloodroot is autogamous (e.g., Schemske 1978). Bloodroots are, or can be, autogamous, but the full story is a bit more complicated.

Notably, bloodroot flowers are protogynous, meaning that the stigmas are receptive to pollen as soon as the flowers open, but the anthers do not shed pollen until sometime later. Literally, protogynous means a first phase female. Studies by D.L. Lyon (1992) show that the female phase can last from one to three days, which coincides with the open-period of any given flower. On day one, petals and stamens spread perpendicular to the pistil, forming a shallow bowl-like configuration. Only a few anthers open on day one. As daylight fades, petals and stamens re-orient upward, closing the flower for the night. Little self-pollination takes place as the flowers close because the anthers do not normally contact the stigma at this point. On day two, if conditions are favorable, flowers re-open and re-assume their bowl-like shape. More anthers dehisce, rendering their pollen available for transfer. As before, flowers close at the end of day two. The events of day three are subtly different: petals reflex, but stamens remain upright. Moreover, as day three progresses, stamens bend inward, bringing their anthers and pollen into

direct contact with the stigma. Thus, autogamy certainly can occur. A few stray pollen grains may reach the stigma on day one or two, but stamen action on day three assures abundant self-pollination. If, however, autogamy is the basic reproductive mode, why wait until day three to consummate the process?

The protogynous character of bloodroot flowers and their undeniable showiness suggest that bloodroot has potential, at least, for outcrossing (xenogamy). The above-mentioned study by Lyon convincingly demonstrates a role for native bees in bloodroot pollination. This study involved careful observation of bloodroot flowers in all sorts of weather, following the fate of individual flowers over multiple days, and a series of controlled experiments involving all combinations of bagged and unbagged flowers, flowers with intact anthers and with anthers removed, and both hand-pollinated and open-pollinated flowers. The bottom line is that when weather conditions are sufficiently warm and dry to permit insect flight, *Andrena carlini* bees are effective pollinators of bloodroot. Upon approaching an open bloodroot flower, the bee lands directly on the stigma and forages for pollen among the anthers surrounding this central spot. Bees spend little time on recently opened flowers with few open anthers; these visits are, however, sufficient to transfer pollen from a previously-visited flower to the stigma. On older flowers, a bee might spend as much as two or three minutes foraging for pollen and, while doing so, it accumulates a load of pollen on the underside of its thorax and abdomen. The bees exhibit good flower constancy, so, upon visiting the next bloodroot flower, pollen from the bee's underside transfers readily to the stigma. Since bloodroot stigmas are receptive from the moment a flower opens, any floral visit by a bee is likely to deliver pollen from another flower and in this way outcrossing (xenogamy) can occur. But if weather conditions are cool and drizzly, if the bees are grounded, after a few days, bloodroot flowers can pollinate themselves, assuring seed production for the year.

Genetically, self-pollination incurs some cost in terms of less genetic diversity among the offspring relative to outcrossed offspring. On average, two parents are likely to encompass more genetic diversity than one. For many reasons, genetic diversity is considered advantageous for the

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VNPS sponsorship gift offers hope to North Carolina botanical friends

Imagine our excitement when we heard that the Virginia Native Plant Society has chosen to "sponsor" a rare plant species that we have been concerned with here at the North Carolina Botanical Garden for many years. The federally endangered harperella (*Ptilimnium nodosum*) is a native of river islands and ponds in scattered locations in the eastern United States. "Sponsorship," in this case is Center for Plant Conservation (CPC) language for an endowment providing an annual sum for recovery efforts.

Harperella, a member of the carrot family (Apiaceae), has 13 remaining populations, down from 26 populations known in 1988. It is found in only one location each in Virginia and North Carolina. The last North Carolina population occurs on the Tar River in Granville County. Two additional North Carolina populations previously occurred along the Deep River at the intersection of Chatham and Lee Counties, but because of severe decline, the eight remaining individuals from this population were rescued in 1997 and brought to the North Carolina Botanical Garden. We now hold approximately 50 descendants of those plants.

Harperella has a number of interesting connections to the Garden. Publications Coordinator Laura Cotterman, while serving as North Carolina Natural Heritage Program botanist, first discovered the Deep River population in the 1980s. Herbarium Curator Alan Weakley contributed to research on the *Ptilimnium nodosum* "complex," conclusions of which support the belief that there are actually three distinct species in this group.

Garden director Peter White and I are supervising the research of University of North Carolina-Chapel Hill graduate student Sarah Marcinko, whose project will explore how land use changes and altered hydrology (e. g., flood water frequency and duration) have contributed to harperella's decline throughout its range. Sarah will also examine the plant's breeding system—or the various means by which this diminutive and reclusive species manages to propagate itself.

Let me not forget to mention that the Tar River Harperella site is just downstream from the home of Assistant Director for Finance Frances Allen! Finally, founding Garden director Ritchie Bell specialized, during his academic career, in plants of the Apiaceae, a family that includes worldwide weeds such as Queen Anne's lace as well as the extremely rare harperella. A recovery goal for Harperella is the successful reintroduction of individuals to the historical location on the banks of the Deep River.

We believe that the conservation of this endangered plant is at a critical juncture, given that extinction seems imminent without human intervention. As a result of our research, we hope to be able to suggest appropriate management techniques for the remaining harperella populations, inform land managers about the plant's recovery needs, and conduct a successful transplantation and restoration project. All of these actions are mandated by the "Harperella Recovery Plan" published by the U. S. Fish and Wildlife Service and are explicit in CPC's mission—"to conserve and restore the rare native plants of the United States."

In 1984 we became a founding Participating Institution of CPC, the only national organization solely dedicated to conserving the germplasm (seeds and whole plants) of the nation's rarest plants. As part of the CPC program, the Garden curates germplasm collections of 34 species from a seven-state area, from Maryland to Mississippi (see the Garden's listing under "Participating Institutions" at www.centerforplantconservation.org). Only 12 of these 34 imperiled plants are sponsored so far, and we welcome the interest of the

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long term success of a species. For example, nature is often patchy; at any given location within a forest, some genetic types may function better than others. Also, the process of long-term adaptation to the environment involves the action of natural selection on genetically variable populations. Bloodroot pollination biology allows for the benefits of cross-pollination, but given the unreliability of the early spring weather and, consequently, the unreliability of its pollinator, self pollination (autogamy) exists as a default or back-up system that assures production of offspring, though these offspring may be somewhat homogeneous in their genetic make-up.

To summarize bloodroot pollination strategy: hurry, wait, and hedge against uncertain fate.

(For more reading, try Lyon, D. L. 1992. "Bee pollination of facultatively xenogamous *Sanguinaria canadensis* L." *Bulletin* Torrey Botanical Club 119: 368-375 and Schemske, D. W. 1978. "Sexual reproduction in an Illinois population of *Sanguinaria canadensis* L." *American Midland Naturalist* 100: 261-268.)

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