The Sex Life of the Red Maple

Richard Primack

Nature has carefully crafted the mating systems of plants and animals to insure genetic diversity in their offspring. Many plants, like some animals, occur as separate male and female individuals to make self-fertilization (which does not promote diversity) less likely. But beyond mere gender differentiation, plants have a wide variety of mating systems. In particular, members of the maple family, Aceraceae, are renowned for their diverse sexual systems; maples run the gamut of sexual reproduction. "Perfect" flowers—those with both stamens and pistils—occur in certain species, such as the Norway maple *(Acer platanoides)*. With perfect flowers self-pollination could occur if the plant's pollen reaches one of its pistils. Other species, such as the box elder *(Acer negundo)*, occur as separate male and female trees; the male trees' flowers have only stamens and the females' flowers only pistils. This separation of the sexes ensures that pollen must move between plants, ruling out self-fertilization.

Between these extremes, we find the especially unusual sexual system of the striped maple *(Acer pensylvanicum)*. Individuals of this species often form clumps of woody shoots that produce male flowers for a few years, followed by female flowers and fruit production for a few years, until the shoot dies. The rootstalk sometimes produces many shoots, each one going through this cycle, keeping the plant alive even though individual shoots die.

Observations were made in a swamp in Newton, Massachusetts. At this site the combination of surface rocks, standing water in winter, and dry conditions in summer limit the size of the trees. As a result, the flowers can be readily observed, and the trees bent over if needed for closer examination.

A branch of red maple female flowers above and below a branch of male flowers. Flowers are produced in clusters of about five at nodes along the twig. Note the male flowers, which have long stamens extending beyond the red petals In these older female flowers, the sides of the ovaries have already begun to take on the characteristic shape of the maple fruit and the stigmas have begun to wilt

Botanists have long studied the reproduction of the red maple tree *(Acer rubrum)*, but until recently there was no consensus on its reproductive biology. The red maple is an abundant, wide-ranging tree of moist woodlands and other habitats. It was described by the Harvard botanist M. L. Fernald (1873–1950) as being "polygamodioecious," meaning that some plants have just male flowers, others just female flowers, and still others have perfect flowers. P. Barry Tomlinson, professor at Harvard University, considered the plant to be "polygamomonoecious," a term indicating that a red maple plant may be entirely male, entirely female, or ambiguous in gender, producing both male and female flowers. Other terms have also been applied to the species. It is the unusual sexual system of the species that causes the confusion in terminology. Individual plants have behaved in perplexing ways: individuals that were thought by naturalists and homeowners to be male trees sometimes produced fruit. The problem was that no one looked at trees in detail over a long enough period to figure out what was going on. Such long-term monitoring is usually not undertaken by taxonomists, who are generally more concerned with developing methods for identifying and classifying species.

As a population biologist, I felt it was important to learn more about the reproductive biology of this common species. Starting in 1979, I monitored 79 small trees for the type and number of flowers that each produced as well as for other demographic characteristics. I checked plants carefully in 1980, 1982, 1983, 1984, and irregularly in subsequent years. All of the trees that I monitored inhabited a rocky, seasonally flooded swamp in which the red maples typically attain a height of only 6 to 30 feet (2 to 10m), allowing all of the flowers to be completely counted and the stems to be bent over for close inspection of flower types.

The site is located in the Hammond Woods, in Newton, Massachusetts, on the west side of the Hammond Pond Parkway. The maples here begin to flower between early and late April, as soon as the weather starts to get warm. The flowers, almost exclusively either male or female, are red to orange to yellowish in color, with five small sepals and petals. They are produced in bunches of about five, with all the flowers in a bunch being either male or female. Male flowers have long, extended stamens with abundant, dusty-yellow pollen and a reduced, nonfunctional pistil. Female flowers have a well-developed ovary, with two long stigmas and reduced, nonfunctional stamens. The length of the stamens and stigmas suggests that the plants are sometimes wind-pollinated, although the flowers are also visited by bees and other insects. Female flowers rapidly develop into flattened, winged fruits with zero, one, or two seeds. The fruits mature quickly and disperse by wind during the summer. Germination is rapid, and there seems to be no seed dormancy.

The 79 trees in my study fell into five gender categories. Fifty-three produced exclusively

A close-up of two flowers, one female, on the left, and the other male. The stigma has begun to wilt in the female flower, and the pollen has been shed from the anthers of the male flower.

male flowers in every year of the study. Another six individuals were inconstant males, producing male flowers exclusively in most years but occasionally producing some female flowers. For example, for four years plant #28 produced only male flowers, but in 1980 it produced 46 male flowers and one female flower. Another plant produced male flowers in every year except 1979, when it produced 37 male and 137 female flowers. Most flowers from these inconstant male trees failed to develop into fruits, no doubt because the plants have a fundamental chromosomal abnormality that prevents fertilization or subsequent fruit development.

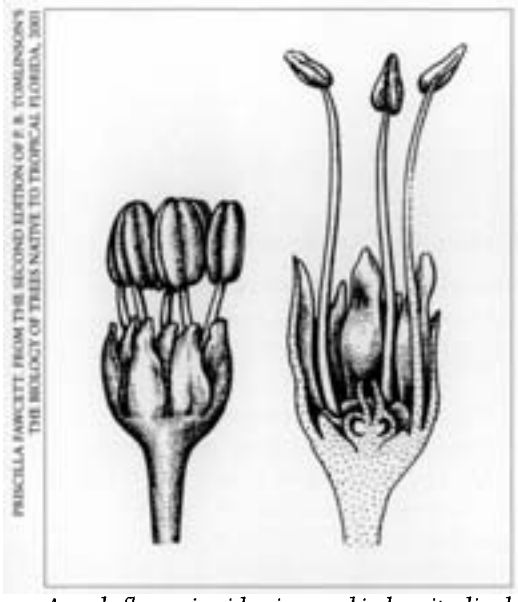
Twelve individuals were constant females, producing only female flowers in every year. Six were inconstant females, producing mostly female flowers in every year with some male flowers in one or more years. And of the 79 plants, two were highly variable in sexual expression, producing only male flowers in some years, only female flowers in other years, and mixtures of male and female flowers in yet other years. Overall, in a typical year the 79 plants produced a total of approximately 21,000 inflorescences of which 18,000 were male and 3,000 were female.

One year I enclosed the flowering branches of some trees in paper bags before they flowered to determine whether the plants were capable of self-pollination or required cross-pollination. All bags contained both male and female flowers. I cross-pollinated some of the bagged flowers using pollen from nearby trees, self-pollinated others using pollen from elsewhere on the same tree, and left others as unpollinated controls. Fruit set was over 90 percent in all three treatments, and most fruits had two seeds. This result indicates that the species is probably capable of automatic self-pollination since experimental self-pollination and cross-pollination did not improve fruit production.

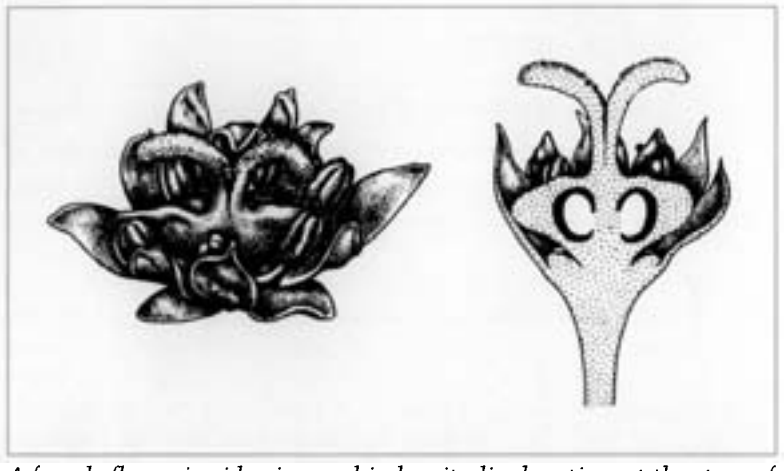
Many of the trees at the study site had two or more stems coming from a common rootstock. In addition to the physical connection, the common origin of stems from a single plant could be identified by the distinctive color patterns of green, red, and yellow on the young leaves. In general, individual stems from the same rootstock confirmed the gender characteristics of the whole plant; that is, in constant male plants, all of the stems had only male flowers, while in constant female plants, all of the stems had only female flowers. However, in the inconstant and variable plants, some individual stems were very different from the others in some years. For example, in 1983 one inconstant female had four flowering stems with percentages of 10, 10, 70, and 83 female flowers, and in 1984 its remaining three flowering stems had percentages of 35, 86, and 89 female flowers.

Growth and reproduction characteristics were compared across plants in the five gender groups. The most instructive difference was that constant female plants were more variable in flower production than were male plants. This makes sense biologically, as female plants producing large numbers of flowers in good years typically go on to produce large numbers of fruit and so may exhaust their energy reserves and be unable to flower well the following year.

Overall, the population is clearly bimodal in sexual expression. Male plants made up 75 percent of the population, 23 percent of the population were females, and 2 percent of the population varied in sex expression. However, of the 77 plants that could be clearly designated as either male or female plants, 12 plants were inconstant in gender and showed at least some evidence of producing flowers of the opposite sex. Such imprecision in dioecious species is known in other species as well; sometimes male plants make a few fruits and female plants



A male flower in side view and in longitudinal section at the stage of pollen dispersal The long stamens are held out beyond the short petals The ovary is small and undeveloped.



A female flower in side view and in longitudinal section, at the stage of pollen receptivity. Note the reduced, nonfunctional stamens and the short petals. The stigma has two branches and is at the top of the flattened ovary The ovary will later develop into the characteristic maple fruit.

produce some male flowers. In this red maple study, individuals of both sexes could produce flowers of the opposite sex. Female plants had a greater tendency for variability than the males, with 33 percent of the females varying in sex expression whereas only 10 percent of the males varied in sex expression.

This study demonstrates the importance of checking for fruit production in investigations of plant gender. For example, inconstant males on occasion produced numerous female flowers, and so these plants were recorded as having some level of female fitness. Yet in some cases very few of the female flowers developed into fruits, indicating a genetic malfunction. Further, certain plants were recorded as having only male flowers even though subsequent checks showed that these plants produced some fruit. It is certainly easier in red maples, and probably in most other species, for a few inconspicuous female flowers to go unnoticed on an otherwise male tree than it is for a few of the conspicuous male flowers—with their strongly extended stamens and yellow anthers—to go unnoticed on an otherwise female tree.

Three unanswered questions remain: What is the genetic basis for the differences between male and female plants? Do all red maple populations include more male plants than female plants? Most important, how many years need a study last to determine these plants' complexities in gender expression?

More work is needed to determine what chromosomal and physiological mechanisms determine sex expression in red maples. More populations need to be studied to determine whether the results obtained in this one population of small individuals are applicable across the range of this widespread and variable species. Field work in this most useful next step in red maple studies requires only a pair of good binoculars, some way of marking or tagging individual trees, and a notebook. And last, studies of sexual expression in red maple need many years to complete. It is clear that a study of one or two years' duration would be inadequate for this species. Careful counting and patience over many years are needed to understand the otherwise confusing patterns of reproduction in this fascinating and ecologically important species.

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