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Most outcrossing plants produce far more flowers than mature fruits. This article views the overproduction of flowers and the subsequent abortion of immature fruits as both a mechanism by which plants can match fruit production to the available resources and as a means of uncoupling the roles of flowers in pollinator attraction and pollen dispersal from their role in seed production. [The *SCI*® indicates that this paper has been cited in more than 315 publications.]

Flower and Fruit Abortion

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This review really began in the spring of 1974 when Wayt Thomas and I, fellow graduate students in botany at the University of Michigan, sat down for a cold drink on his porch following a departmental softball game. As it was early May, the horse chestnuts and apples were in full bloom. The sheer exuberance of their floral display made us wonder why these plants would produce so many flowers when only 1 in 20 or so would produce a mature fruit. What could account for the evolution and maintenance of such an apparently inefficient reproductive system?

Over the next several years, I began to search for clues. I learned that most outcrossing plants (not just apples and horse chestnuts) are physiologically incapable of providing the necessary resources to develop mature fruits from all of the flowers they produce; that immature fruits abort when the number of pollinated flowers exceeds the resources available for fruit production; that aspects of fruit abortion have been investigated by physiologists, horticulturalists, foresters, and others in the plant sciences since the turn of the century; and that Wayt and I were only among the latest in a line of biologists, from C. Darwin[1] to D.H. Janzen,[2] who pondered the evolution of this common but enigmatic reproductive system.

The review was written in the middle of nearly two decades of clever experimentation that went a long way toward solving the mystery. Following the lead of M.F. Willson and B.J. Rathcke,[3] several studies showed that the "surplus" flowers attract pollinators and increase the amount of a plant's pollen that is removed, thereby decreasing the chance that a plant's seed crop would be limited by its ability to garner pollen while simultaneously increasing a plant's chances of siring seeds on conspecifics. Other studies focused on which of the immature fruits would mature and which would abort. These studies found that fruit abortion is nonrandom with respect to damage (such as that caused by seed predators and bad weather) and with respect to the number of seeds within a fruit (the more the better). These patterns of abortion tended to conserve resources by culling offspring that were unlikely to mature and by improving the efficiency of seed packaging within fruits. Moreover, Darwin,[1] Janzen,[2] and E.L. Charnov,[4] each using different lines of reasoning, hypothesized that plants could improve offspring quality by the nonrandom abortion of fruits—a lead that was explored and confirmed in the decade since the review. In short, this reproductive pattern isn't as inefficient as was tacitly assumed. It probably increases a plant's reproductive output through the combined male and female functions (though not yet directly demonstrated), and it improves the average quality of a plant's seed crop.

A portion of the success of this review is due to Sam Smith, a plant pathologist whose office was directly below mine and who, like me, was prone to writing at night. Sam advised me "not to write just another review" but rather "to use the literature to tell a story." The resulting "whodunit" story synthesized the efforts of plant biologists from many disciplines and, almost inadvertently, seems to have touched upon many issues of debate over the past decade. If the story were retold today, it would be far richer with examples, more firmly rooted in formal theory, and more closely tied to the larger issues of life-history evolution, phenotypic plasticity, and gene flow.[5-7] The original story, however, organized many of the clues that have proven to be useful, but it is premature to declare the mystery solved.

1. **Darwin C.** *The effects of cross- and self-fertilisation in the vegetable kingdom.* London, England: Murray, 1876. 482 p. (Cited 200 times since 1945.)
2. **Janzen D H.** A note on optimal mate selection by plants. *Amer. Naturalist* 111:365-71, 1977. (Cited 110 times.)
3. **Willson M F & Rathcke B J.** Adaptive design of the floral display in *Asclepias syriaca* L. *Amer. Midland Naturalist* 92:47-57, 1974. (Cited 115 times.)
4. **Charnov E L.** Simultaneous hermaphroditism and sexual selection. *Proc. Nat. Acad. Sci. USA* 76:2480-4, 1979. (Cited 160 times.)
5. **Kozlowski J & Stearns S C.** Hypotheses for the production of excess zygotes: models of bet-hedging and selective abortion. *Evolution* 43:1369-77, 1989.
6. **Ehrlen J.** Why do plants produce surplus flowers? A reserve-ovary model. *Amer. Naturalist* 138:918-33, 1991.
7. **Schlichting C D.** The evolution of phenotypic plasticity in plants. *Annu. Rev. Ecol. Syst.* 17:667-93, 1986.

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