## POLLINATOR LIMITATION OF PLANT REPRODUCTIVE EFFORT

In many recent studies there have been attempts to describe and explain patterns of resource allocation in plants (e.g., Abrahamson and Gadgil 1973; Newell and Tramer 1978). Nearly all such studies are based on the unstated assumption that the reproductive output of a plant is resource limited.

However, if hand-pollinated plants produce more seeds than naturally pollinated controls, then reproduction is being limited, not by energy levels, but by pollinator activity. As part of a study on the population biology of *Arisaema triphyllum*, a herbaceous forest perennial (Bierzychudek 1981), I hand pollinated some plants in a natural population. The difference between hand-pollinated and natural seed production was remarkably large. Hand-pollinated plants produced over an order of magnitude more seeds (the mean for medium-sized plants was 43.2 seeds/plant, $N = 12$) than did controls of similar size (mean = 1.0, $N = 20$). While there was no relationship between the size of a plant and the number of seeds it produced when naturally pollinated ($r = .11$, $N = 35$), this same relationship was significant for hand-pollinated plants ($r = .81$, $N = 33$, $P < .01$), indicating that only the hand-pollinated individuals were resource limited. There is no reason to assume that this level of seed production is unusually low for *Arisaema*; I observed only slightly higher levels at several other sites and in other years (with a maximum of 10.3 seeds/plant). *Arisaema*'s pollinators (mycetophilid and sciarid flies) seem abundant, if not particularly efficient. Others have observed similar low rates of seed production by *Arisaema* (Meehan 1886; Sakamoto 1961; Treiber 1980).

Is this an isolated case, or do pollinators limit the reproductive output of many plants? The yield of many cultivated crop plants has been found to be pollinator limited (McGregor 1976), but this might be expected when large plantings are made of a single crop species. Information on native species under natural conditions is more difficult to find. Schemske et al. (1978) note that only 33% of naturally pollinated flowers of *Erythronium albidum* set seed, compared with 78% of flowers outcrossed by hand. Willson et al. (1979) show that 82.3% of hand-outcrossed *Phlox divaricata* produced some seed, compared to 58% of naturally pollinated plants at the same site. In Costa Rica 29.7% of hand-outcrossed flowers of *Combretum fruticosum* set fruit, compared to 7% of naturally pollinated flowers (Schemske, in press). *Brassavola nodosa*, a Central American orchid, also seems to be pollinator limited: 67% of hand-outcrossed flowers set fruit, versus 12% of naturally pollinated flowers (Schemske 1980). Weller (1980) found the fecundity of hand-pollinated *Lithospermum caroliniense* averaged 17% compared to 9% for naturally pollinated individuals, a significant difference. Finally, *Encyclia cordigera*, another orchid, may also be pollinator limited: Among hand-pollinated inflorescences, the proportion producing no fruit ranged from 5% to 22%, depending on the identity of the pollen donors. Seventy-eight percent of naturally pollinated inflorescences set no fruit (Janzen et al. 1980).

The results of some hand pollination experiments are quite different. Stephenson (1979) found that hand-pollinated *Catalpa speciosa* produced significantly

Am. Nat. 1981. Vol. 117, pp. 838–840.

fewer fruits per inflorescence (2.35 ± 1.60) than naturally pollinated plants did (2.68 ± 1.88), though fruits resulting from hand pollination contained more seeds. Willson et al. (1979) observed a lower percentage of seed set for hand-pollinated *Geranium maculatum* than for naturally pollinated plants. And Waser (1978) found that two Rocky Mountain hummingbird-pollinated herbs, *Ipomopsis aggregata* and *Delphinium nelsoni*, produced more seeds naturally than when hand pollinated (10.2 seeds/flower vs. 5.5–9.9 seeds/flower for *Ipomopsis*; 49.5 seeds/flower vs. 11.5–16.6 seeds/flower for *Delphinium*). For these cases in which hand pollination was not as successful as natural pollination, it appears that the treatment itself had some detrimental effects; otherwise the results of hand pollination and natural pollination would be expected to be indistinguishable, as Primack and Lloyd (1980) found for *Leptospermum scoparium*, a New Zealand shrub.

Janzen et al. (1980) caution against interpreting data from one year's seed or fruit production as evidence of pollinator limitation. They argue that hand pollinations must produce higher than natural fecundity levels over a period of several years before the resource-limitation hypothesis can be discarded, because the "cost" of one heavy fruiting year may only be apparent when the plant fails to reproduce the following year. Only the data from *Arisaema* can be assessed by this criterion. Plants were divided into two groups, those that produced 10 or fewer seeds/plant (10.3 was the maximum average seed production observed for naturally pollinated individuals), and those that produced more than 10 seeds/plant (range = 26–127). These two groups of plants did not differ in their mean size. *Arisaema* plants can change sex, and females can compensate for leaf damage or the cost of seed production by flowering as males or not at all in subsequent years (Bierzychudek 1981). The proportion of plants remaining female the next year was no less (75%, $N = 8$) for plants that had produced many seeds than for plants that had produced few (61%, $N = 28$). At least for *Arisaema triphyllum*, reproduction is truly pollinator limited.

While certainly not all species are pollinator limited, pollinator limitation of reproductive output seems to be a common phenomenon. It is important that studies of resource allocation recognize this possibility. Most studies performed thus far have ignored the possible influence of pollinator limitation (a notable exception is van Andel and Vera 1977). But without considering the effect of pollinators, two sorts of findings may be in error. First, it is often concluded that populations of the same plant species in different habitats have different patterns of resource allocation (e.g., Abrahamson and Gadgil 1973; Abrahamson 1975; Hickman 1975). This may be a spurious conclusion if pollinator efficiency also differs between habitats. Second, pollinator-limited individuals probably commit less resources to seeds and more to flowers than they would if they were resource limited. This will affect field or greenhouse studies concerned with measuring how energy is allocated to different components of reproduction; such measurements will be in error when pollinators are limiting.

ACKNOWLEDGMENTS

I am grateful for the improvements suggested by Richard B. Root, Peter Kareiva, Andrew Stephenson, and an anonymous reviewer, and to Douglas

Schemske and Steven Weller for providing unpublished data. This research was supported in part by a Sigma Xi Grant-in-Aid of Research, and by Cornell University's Section of Ecology and Systematics.

LITERATURE CITED

Abrahamson, W. G. 1975. Reproductive strategies in dewberries. Ecology 56:721–726.

Abrahamson, W. G., and M. D. Gadgil. 1973. Growth form and reproductive effort in goldenrods (*Solidago*, Compositae). Am. Nat. 107:651–661.

Andel, J. van, and F. Vera. 1977. Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition. J. Ecol. 65:747–758.

Bierzychudek, P. 1981. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ph.D. diss. Cornell University.

Hickman, J. C. 1975. Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense* (Polygonaceae). J. Ecol. 63:689–701.

Janzen, D. H., P. DeVries, D. E. Gladstone, M. L. Higgins, and T. M. Lewisohn. 1980. Self- and cross-pollination of *Encyclia cordigera* (Orchidaceae) in Santa Rosa National Park, Costa Rica. Biotropica 12(1):72–74.

McGregor, S. E. 1976. Insect pollination of cultivated crop plants. Agriculture Handbook No. 496, Agric. Res. Ser. USDA.

Meehan, T. 1886. Notes on *Arisaema triphyllum*. Bot. Gaz. xi:217.

Newell, S. J., and E. J. Tramer. 1978. Reproductive strategies in herbaceous plant communities during succession. Ecology 59:228–234.

Primack, R. B., and D. G. Lloyd. 1980. Andromonoecy in the New Zealand shrub manuka, *Leptospermum scoparium* (Myrtaceae). Am. J. Bot. 67:361–368.

Sakamoto, S. 1961. *Arisaema triphyllum*, jack-in-the-pulpit, in Minnesota, especially at the Cedar Creek Natural History Area. Proc. Minn. Acad. Sci. 29:153–168.

Schemske, D. E. 1980. Evolution of floral display in the orchid *Brassavola nodosa*. Evolution 34:489–493.

———. In press. Floral ecology and hummingbird pollination of *Combretum fruticosum* in Costa Rica. Biotropica.

Schemske, D. E., M. F. Willson, M. N. Melampy, L. J. Miller, L. Verner, K. M. Schemske, and L. B. Best. 1978. Flowering ecology of some spring woodland herbs. Ecology 59:351–366.

Stephenson, A. G. 1979. An evolutionary examination of the floral display of *Catalpa speciosa* (Bignoniaceae). Evolution 33:1200–1209.

Treiber, M. 1980. Biosystematics of the *Arisaema triphyllum* complex. Ph.D. diss. University of North Carolina, Chapel Hill.

Waser, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. Ecology 59:934–944.

Weller, S. G. 1980. Pollen flow and fecundity in populations of *Lithospermum caroliniense*. Am. J. Bot. 67:1334–1341.

Willson, M. F., L. J. Miller, and B. J. Rathcke. 1979. Floral display in *Phlox* and *Geranium*: adaptive aspects. Evolution 33:52–63.

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