

COSTS OF FLOWER AND FRUIT PRODUCTION IN *TIPULARIA DISCOLOR* (ORCHIDACEAE)¹

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Abstract. The cost of reproduction may be an important constraint on the evolution of life history traits, yet it has seldom been adequately measured in plants. To demonstrate a net cost of reproductive structures one must show that their production has a negative effect on future growth. Using a summer-deciduous orchid, we compared subsequent growth of plants with no inflorescence, no fruits, few fruits (≤ 10), or many fruits (> 10). Greater investment in reproduction led to increasingly negative effects on future corm size and leaf area. The cost of an inflorescence without fruits was about one-half the cost of an inflorescence with few fruits. Each fruit cost the plant $\approx 2\%$ of its total leaf area the next year. Natural pollination resulted in a mean of seven fruits per plant. Hand-pollination led to a dramatic increase in fruit set (up to 25 fruits per plant), and a large decrease in subsequent growth. Plants with many fruits were less likely to propagate vegetatively than those with few fruits. Also, plants with many fruits were less likely to flower the following year, probably because they were smaller than those with few fruits. The potential benefits of greater pollinator visitation are unclear because larger "clutch size" may not result in greater lifetime fecundity.

Key words: *clonal; corm growth; fruit set; inflorescence; life history patterns; plant size; pollen-limitation; pollination; orchid; reproductive costs; Tipularia discolor.*

INTRODUCTION

A basic tenet of life history theory is that traits such as clutch size and the frequency of reproduction have evolved to maximize an organism's lifetime fitness (Stearns 1977). If reproductive episodes divert resources from an organism's maintenance and growth, this cost can represent a constraint on the evolution of possible life history traits (Williams 1966, Pianka and Parker 1975, Charnov 1982). In plants, allocation of resources to reproduction may occur at the expense of future vegetative growth, which in turn could alter competitive ability, susceptibility to predation, vegetative propagation, and other characteristics that affect survivorship and lifetime fecundity.

It is widely assumed that flowering and fruit set occur at the expense of future growth. Quantifying the costs of reproduction, however, can be problematic (Thompson and Stewart 1981, Reekie and Bazzaz 1987*a, b, c*). Two approaches have been used to assess the cost of reproduction in plants. One involves estimating the proportion of limiting resources, such as carbon or nutrients, that are allocated to reproductive structures (Harper 1977, Bloom et al. 1985, Jurik 1985). This proportion is often referred to as a plant's reproductive effort (Thompson and Stewart 1981). The other method is to determine whether reproductive events lead to a decrease in future growth, reproduction, and survivorship.

Most studies of the cost of reproduction employ the first approach, since carbon allocation, in particular, can easily be estimated in terms of biomass. One problem with this technique is that carbon allocation may not accurately reflect the distribution of limiting nutrients, which may be concentrated in seeds or other plant parts (Lovett Doust 1980, Thompson and Stewart 1981). In many species, however, general patterns of carbon allocation are well correlated with the distribution of macronutrients (Abrahamson and Caswell 1982, data in Whigham 1984, Reekie and Bazzaz 1987*b*). A more serious problem with using carbon as the currency for measuring reproductive costs is that flowers, fruits, and their supporting structures can sometimes carry on photosynthesis (Bazzaz et al. 1979, Alpert et al. 1985, Jurik 1985, Williams et al. 1985). These organs may therefore be partially self sufficient and may even stimulate photosynthetic rates of nearby leaves (Neales and Incoll 1968, Reekie and Bazzaz 1987*a*). In some cases, then, direct measurements of biomass allocation would overestimate the cost of seed production to the parent plant, leading to erroneous conclusions about trade-offs between reproduction and future growth. Species also vary in their ability to recover nutrients and nonstructural carbon invested in reproductive organs (Chapin 1980, Whigham 1984). Unless allocation to one structure or activity occurs at the expense of another, it is difficult to make predictions about the evolutionary causes and ecological consequences of different allocation patterns (Harper 1977).

Ultimately, then, the best way to assess the net cost of reproduction is to test for an associated decrease in subsequent growth. Although relatively few investi-

¹ Manuscript received 30 June 1988; revised 22 November 1988; accepted 30 November 1988.

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gators have followed this approach, most who did have found that producing offspring is costly. Flower and fruit production led to a decrease in growth in several conifers (Eis et al. 1965), *Podophyllum peltatum* (Sohn and Policansky 1977), *Poa annua* (Law 1979), and *Plantago lanceolata* (Antonovics 1980), and to earlier mortality in *Poa annua* (Law 1979) and *Senecio keniodendron* (Smith and Young 1982). Individuals of several orchid species were smaller after reproducing (see Discussion). Reproduction did not lead to reduced growth in laboratory-grown *Agropyron repens* (Reekie and Bazzaz 1987b).

The separate costs of flower and fruit production can be determined by comparing the subsequent growth of flowering plants that set fruit with those that do not. Fruit set reduced subsequent growth in *Podophyllum peltatum* (Sohn and Policansky 1977) and *Asclepias quadrifolia* (Chaplin and Walker 1982), but not in dioecious *Acer negundo* (Willson 1986). Bierzychudek (1984) found that female jack-in-the-pulpits that produced fruits were more likely to become males than nonfruiting females, and males were typically smaller than females. When *Ipomopsis aggregata* individuals failed to set fruit, they shifted from the normal semelparous mode of reproduction to iteroparous reproduction (Paige and Whitham 1987). Costs of high fruit set are avoided to some extent by species that abort pollinated flowers or young fruits (Lloyd 1980, Stephenson 1981).

These results clearly indicate that the cost of reproduction varies among species. This occurs for several reasons. First, the proportion of a plant's biomass that is allocated to reproductive structures varies widely among species (Harper 1977). Also, the phenology of flowering and fruiting is seasonally variable among species, and these events do not always correspond to times of greatest photosynthetic activity or resource availability. Finally, reproductive structures vary in their ability to photosynthesize and to translocate resources back to the parent plant.

Here we report results from experimental studies of the net costs of reproduction in the crane fly orchid, *Tipularia discolor*. Our aim was to assess the relative costs of inflorescences and fruits under natural conditions. The specific questions we addressed were:

- 1) What levels of fruit set occur in natural populations?
- 2) Is fruit set regulated by pollinator service?
- 3) How does the cost of producing only an inflorescence compare with that of achieving low vs. high levels of fruit set?

MATERIALS AND METHODS

Tipularia discolor (Pursh) Nutt. is a common woodland orchid in the southeastern United States. Individual plants typically consist of a single leaf, which emerges in the fall and produces a corm at its base by

the following spring (Fig. 1). Corms occur near the soil surface and usually persist for 2–3 yr. This growth form makes it easy to measure leaf area, total plant size, and net annual carbon gain (corms can be excavated, measured, and replaced nondestructively).

Plants are leafless throughout the summer. In July, corms that are sufficiently large produce inflorescences of 20–30 flowers. Animal vectors (noctuid moths) are required for pollen transfer (Stoutamire 1978, Whigham and McWethy 1980). *Tipularia* is self-compatible (Whigham and McWethy 1980) but selfing is probably rare because extracted pollinia are initially covered by a thin cap. Pollinia will not adhere to stigmas until the cap falls off, at least 30 min after extraction (A. Snow, personal observation). Fruits mature by October and release thousands of dust-like seeds. Reproductive structures including fruits comprise $\approx 20\%$ of a plant's dry mass (data from naturally pollinated plants, older corms included, Whigham 1984).

Just prior to forest leaf fall, each corm produces one or occasionally two new leaves. Primary and smaller secondary leaves arise from opposite ends of the corm (Fig. 1). When two leaves are produced, the corm that connects them disintegrates within a few years, so close neighbors may be ramets from the same parent. (Seedling recruitment near mature plants has never been observed in an ongoing 11-yr study of permanently marked plants [Whigham and O'Neill 1988].) Corm growth and clonal propagation in South Carolina populations of *Tipularia* were described in detail by Efrid (1987).

We studied two populations of *Tipularia* in deciduous forests at the Smithsonian Environmental Research Center, near Edgewater, Maryland, USA. The populations were ≈ 1.2 km apart. Costs of flower and fruit production were measured at Site 1 only. In 1987 we labelled 120 flowering plants at Site 1 and assigned them to one of three treatments: no fruit (pollinated flowers removed), natural pollination, or hand-pollination (every flower received pollen from another plant). A fourth "treatment" consisted of 40 large vegetative plants (nonflowering). Whenever possible, each of the four treatments was assigned at random within a group of neighboring plants, so replicates came from similar microsites.

These treatments allowed us to compare the effects of having an inflorescence only, having few fruits, or having many fruits on subsequent leaf area and corm size the following May. Plants with damaged leaves or shrivelled corms were not used. Leaf area (in square centimetres) was calculated by entering length (L) and width (W) in the regression $Y = 0.71(L \times W) - 6.87$ ($R^2 = 0.99$, $N = 33$). Corm dry mass (in milligrams) was also estimated nondestructively by using corm length (L), width (W), and height (H) in the regression $Y = 0.182(L \times W \times H) + 31.90$ ($R^2 = 0.97$, $N = 33$). If a plant produced two leaves (and therefore two corms), data from the two branches were summed for analyses.



FIG. 1. The annual growth cycle of *Tipularia discolor* during a reproductive year. IL = initial leaf, IC = initial corm produced by IL, B = inflorescence bud, FL = flowers, FR = fruits, NL = new primary leaf, NC = new corm being produced by NL. Dotted line indicates where a secondary leaf sometimes arises to form a new branch.

The previous year's corm (Fig. 1) was also measured so that initial corm size could be used as a covariate in analyses of variance. One year after the pollination treatments were used, we noted whether experimental plants with undamaged leaves flowered again, i.e., in two consecutive years.

We compared a subset of the treatments, natural vs. hand-pollination, to determine whether fruit set was limited by pollinator service. These two treatments were used at both Site 1 (1986, 1987) and Site 2 (1987). To increase our sample size for characterizing natural levels of fruit set, we recorded fruit set on a total of 151 additional unmanipulated plants (both years at Site 1, 1987 at Site 2).

Sexual reproduction had a negative effect on future plant size, so we also investigated the relationship between plant size and the likelihood of flowering. Beginning in 1982, we censused all individuals in 35 groups of plants at Site 1 ($N = 114$ plants). Within a group, individuals were <0.5 m apart and probably represented ramets from the same genet. From 1982 through 1987 (excluding 1985), we measured leaf area each spring and noted whether the plant flowered the next summer. About half of the plants died by 1987, usually

due to predation by deer or rodents (Whigham and O'Neill 1988).

RESULTS

Natural fruit set

Flower and fruit number were remarkably consistent across years and sites, averaging 30 flowers and 6–8 fruits per naturally pollinated plant (Table 1). For all unmanipulated plants censused in both years, the mean (± 1 SE) number of fruits per plant was 6.7 ± 0.3 ($N = 268$). Only 11% of these plants failed to set fruit; 68% produced 1–10 fruits, and 6% produced >15 fruits. In our analyses of the cost of fruit production, we designated plants with >10 fruits as those with high fruit set.

Augmented fruit set

Hand-pollination led to a dramatic increase in fruit set, especially in 1986, when $\approx 90\%$ of all pollinated flowers set fruit (Table 1). In 1987, when a drought occurred before and during the flowering period, many flowers wilted and some young fruits aborted. This did not result in fewer fruits on control plants (relative to

TABLE 1. Fruit set on unmanipulated controls and hand-pollinated (augmented) inflorescences. Means \pm 1 SE; treatment effects on number of fruits within sites and years were significant at $P < .001$ (t tests).

	<i>N</i>	Percent flowers setting fruit	Number of fruits	Number of flowers
Site 1, 1986				
Control	39	18 \pm 2	5.6 \pm 0.7	30.9 \pm 0.9
Augmented	39	89 \pm 1	27.3 \pm 0.9	30.6 \pm 0.9
Site 1, 1987				
Control	39	25 \pm 3	7.7 \pm 1.0	30.7 \pm 1.2
Augmented	38	64 \pm 3	19.7 \pm 1.0	30.7 \pm 0.8
Site 2, 1987				
Control	39	23 \pm 3	6.9 \pm 1.0	30.3 \pm 1.0
Augmented	46	47 \pm 3	13.2 \pm 0.8	29.1 \pm 0.9

1986), but only 47–64% of the hand-pollinated flowers set fruit. Even so, these plants typically produced > 10 mature fruits, and the effect of hand-pollination was highly significant (Table 1).

Effects of reproduction on plant size

Flower and fruit production had a strong negative effect on subsequent growth. While vegetative plants doubled the size of their most recent corm from one year to the next, those with high fruit set produced a smaller corm during the same interval (Fig. 2, Table 2). On plants with 1–10 fruits, representing most naturally pollinated individuals, the most recent corm remained about the same size before and after reproducing in both 1986 and 1987. The cost of producing an inflorescence was about one-half that of producing 1–10 fruits (relative to vegetative plants, Fig. 2).

Reproduction had a similar negative effect on total leaf area (Table 2). Primary leaves of plants with few and many fruits in 1987 were 14 and 46% smaller than those with flowers but without fruit. As expected, leaf area was well correlated with the mass of the subtending corm ($R^2 = 0.83$, $n = 91$). Treatment effects on leaf area and corm mass were not confounded by pretreatment differences in corm size: initial corm mass did not vary significantly among treatments (Tukey test, 100 df). Within treatments, however, initial corm mass did explain a significant amount of the variation in leaf area and new corm mass (ANCOVA for Table 2).

Frequency of subsequent flowering

Plants with low levels of fruit set were more likely to produce an inflorescence the next year than those with many fruits. Twenty-three percent ($N = 43$) of the individuals with ≤ 10 fruits flowered the next year, while only 3% ($N = 32$) of those with > 10 fruits did so ($G = 6.86$, $P < .01$). The average interval (\pm SE) between flowering events for naturally pollinated plants was 2.5 ± 0.4 yr ($N = 32$; D. F. Whigham, *personal observation*). These plants, which were sometimes

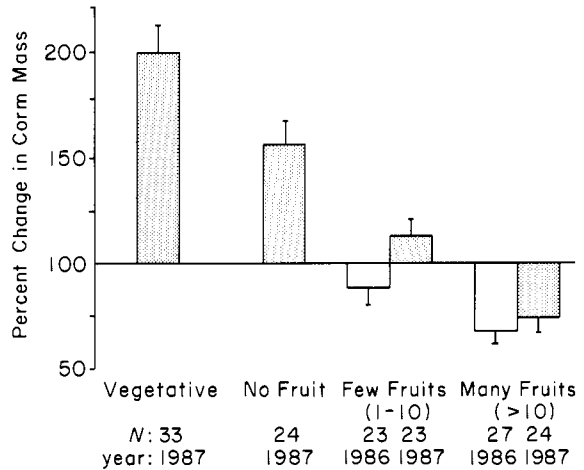


FIG. 2. Effects of flower and fruit production on percent change in corm mass (means \pm 1 SE). Mean (\pm 1 SE) number of fruits per plant for low vs. high fruit set were 5.1 ± 0.6 vs. 24.9 ± 1.2 in 1986, and 6.0 ± 0.7 vs. 18.7 ± 1.3 in 1987. Differences between pairs of means (arcsine-transformed) were compared using CONTRAST tests following ANOVA (SAS 1985, 1 df): for vegetative vs. no fruit $F = 6.96$, $P < .01$; no fruit vs. few fruits $F = 5.00$, $P < .03$; few fruits vs. many $F = 2.54$, ns in 1986; $F = 3.52$, $P < .06$ in 1987.

damaged by mammalian herbivores, probably required a longer interval to recover from reproductive costs than did our experimental plants, which had intact leaves.

Further evidence that high fruit set led to delayed flowering can be inferred from the negative effect of fruit set on leaf area the following year. Data from 1982 to 1987 show that the proportion of plants that produced an inflorescence increased with leaf area (Table 3). The minimum size at which plants flowered varied from year to year, but it is clear that large plants were more likely to flower than were small ones. On our experimental plants with high fruit set, subsequent area of the primary leaf was ≈ 10 cm² less than that of plants that did not bear fruit (12.1 vs. 22.5 cm²; Table 2). Table 3 shows that an effect of this magnitude should be great enough to influence the probability of flowering the next year.

Frequency of subsequent branching

None of the vegetative plants branched, although this sometimes occurs in other populations (Efrd 1987). Fifty-seven percent of the unmanipulated flowering plants produced two leaves in 1986 and 66% did so in 1987 ($N = 88, 107$). Plants that branched became much larger than those that did not (Table 4). In 1986, plants that branched had significantly larger initial corm sizes than those producing a single leaf. Also, low fruit set appeared to promote subsequent branching. Branching occurred in 75% of the plants without fruits, 50% of those with low fruit set, and 34% of those with high fruit set (test of independence: $G = 11.92$, $P < .01$;

TABLE 2. Effects of sexual reproduction on future growth in *Tipularia*. Sample sizes as in Fig. 2. One-way ANOVAs and ANCOVAs were conducted, with initial corm size as a covariate for new corm mass (mg) and leaf area (cm²). *F* values for 1987 data are from a priori comparisons between means using a CONTRAST test in SAS with 1 df (SAS 1985).

A. Effects of flowering						
1987	Vegetative		Inflorescence with no fruit		<i>F</i>	<i>P</i>
	\bar{X}	(SE)	\bar{X}	(SE)		
Initial corm mass (mg)	474	(28)	488	(33)	0.07	NS
New corm mass (mg)	913	(69)	743	(61)	6.69	.01
Total leaf area (cm ²)	24.3	(1.2)	27.7	(1.9)	2.58	NS
Area of primary leaf (cm ²)	24.3	(1.2)	22.5	(1.5)	1.69	NS

B. Effects of few fruits (1–10 per plant)						
1987	Inflorescence with				<i>F</i>	<i>P</i>
	No fruit		Few fruits			
	\bar{X}	(SE)	\bar{X}	(SE)		
Initial corm mass (mg)	488	(33)	583	(42)	2.54	NS
New corm mass (mg)	743	(61)	664	(55)	4.86	.03
Total leaf area (cm ²)	27.7	(1.9)	22.7	(1.6)	11.95	.001
Area of primary leaf (cm ²)	22.5	(1.5)	19.5	(1.7)	7.24	.01

C. Effects of many fruits (> 10 per plant)						
1986	Inflorescence with				<i>F</i>	<i>P</i>
	Few fruits		Many fruits			
	\bar{X}	(SE)	\bar{X}	(SE)		
Initial corm mass (mg)	608	(35)	581	(37)	0.29	NS
New corm mass (mg)	597	(72)	429	(43)	4.43	.04
Total leaf area (cm ²)	20.3	(2.3)	13.9	(1.6)	4.36	.04
Area of primary leaf (cm ²)	16.1	(1.7)	12.1	(1.1)	4.45	.04

1987	Inflorescence with				<i>F</i>	<i>P</i>
	Few fruits		Many fruits			
	\bar{X}	(SE)	\bar{X}	(SE)		
Initial corm mass (mg)	583	(42)	576	(57)	0.29	NS
New corm mass (mg)	664	(55)	482	(68)	5.02	.03
Total leaf area (cm ²)	22.7	(1.6)	15.2	(2.2)	12.39	.001
Area of primary leaf (cm ²)	19.5	(1.7)	12.1	(1.5)	16.37	.001

data from both years were pooled because differences between years were statistically homogeneous [$G = 1.09$, data from plants with ≥ 1 fruit]).

DISCUSSION

In *Tipularia discolor*, flowering and fruiting clearly depleted stored reserves that would otherwise be al-

located to growth the following year (Fig. 2). Vegetative plants grew more than flowering ones. Plants with low fruit set, which is typical, remained relatively constant in size, but showed a significant decrease in new leaf area and corm mass relative to nonfruiting plants. This demonstrates a negative effect of natural levels of fruit production on future growth. Plants with unusually high fruit set (> 10 fruits) actually produced a smaller leaf and corm in the year after flowering as compared to the year before flowering.

These costs of reproduction would have been misrepresented if we had used the biomass of inflorescences and fruits to estimate them. For example, the effects of few vs. many fruits on corm size were greater in 1987, when the plants showed a threefold difference in fruit number, than they were in 1986, when there was a fivefold difference in average fruit number for each treatment (Fig. 2). The cost of allocating a given amount of biomass to each fruit probably varies between years and across sites (Jurik 1985).

Another consequence of high fruit set was reduced vegetative propagation. More than one-half of all flowering plants branched by producing a smaller secondary leaf. The probability of branching was greater for

TABLE 3. Proportion of plants that flowered, as a function of leaf area the previous spring. Sample size for each size class is given in parentheses; frequencies within years were used in tests of independence.

Year	Leaf area (cm ²)				<i>G</i>	<i>P</i>
	1–10	11–20	21–30	>30		
1982	0.00 (38)	0.08 (49)	0.50 (16)	0.27 (11)	26.00	.001
1983	0.03 (35)	0.16 (45)	0.14 (21)	0.43 (7)	7.85	.05
1984	0.09 (35)	0.08 (25)	0.27 (15)	0.67 (6)	11.91	.01
1986	0.00 (25)	0.14 (29)	0.22 (9)	0.60 (10)	18.98	.001
1987	0.00 (19)	0.07 (15)	0.25 (12)	0.33 (9)	9.63	.05

TABLE 4. Comparisons between flowering plants that did not branch (one leaf) with those that did (two leaves) at Site 1. Flowering and fruiting occurred prior to the production of leaves and corms, with the exception of the initial corm. Data are from plants used in Fig. 2.

1986	1 leaf (N = 30)		2 leaves (N = 20)		
Number of plants with:					
1-10 fruits	12		11		
> 10 fruits	18		9		
	\bar{X}	(SE)	\bar{X}	(SE)	P*
Flowers per plant	28.2	(0.9)	30.1	(1.1)	NS
Initial corm mass (mg)	547	(86)	663	(47)	.02
New corm mass (mg)	377	(28)	700	(79)	.0001
Total leaf area (cm ²)	12.0	(1.1)	23.0	(2.4)	.001
Area of primary leaf (cm ²)	12.0	(1.1)	16.9	(1.9)	.01
1987	1 leaf (N = 29)		2 leaves (N = 42)		
Number of plants with:					
0 fruits	6		18		
1-10 fruits	11		12		
> 10 fruits	12		12		
	\bar{X}	(SE)	\bar{X}	(SE)	P
Flowers per plant	25.7	(2.4)	25.6	(2.0)	NS
Initial corm mass (mg)	538	(35)	558	(37)	NS
New corm mass (mg)	514	(51)	709	(49)	.008
Total leaf area (cm ²)	17.1	(1.8)	25.1	(1.5)	.001
Area of primary leaf (cm ²)	17.1	(1.8)	18.6	(1.3)	NS

* Significant differences between means were determined by *t* tests.

plants with more available reserves: those with fewer fruits and those that were larger initially. Sohn and Policansky (1977) also found a negative effect of fruit set on branching in rhizomatous *Podophyllum peltatum*, which produces a single large fruit. Branching appears to regulate the maximum size of ramets in these species, and probably prolongs the life of individuals clones by spreading the risk of mortality over space (e.g., Cook 1979). In addition, neighboring inflorescences of plants from the same genet could serve to attract pollinators (e.g., Firmage and Cole 1988).

Our results show that natural variation in pollinator-mediated fruit set can influence the frequency of flowering in *Tipularia*. We found that the probability of flowering increased with leaf area (see also Efrid 1987). Therefore, it is not surprising that plants with few fruits (and larger leaves) were more likely to flower in consecutive years than those with many fruits. Thus, the potential benefits of higher fruit set in a given year may be offset by having fewer reproductive episodes as well as less clonal propagation. However, the fitness trade-offs between greater "clutch size" and fewer "clutches" depend on the potential advantages of earlier reproduction (Cole 1954, Schaffer and Gadgil 1975). Without a better understanding of age-specific fecundity and survivorship schedules, for both parents and their clonal descendants, it is difficult to determine whether lifetime reproduction is pollen limited in *Tipularia*. At this point, we can only conclude that short-term hand-pollination experiments are not adequate for assessing pollen limitation of lifetime reproductive success.

Orchids are characterized by having highly specialized flowers and low levels of fruit set in nature (Darwin 1887). Higher fruit set following hand-pollination is common (reviewed in Zimmerman and Aide 1989), but studies such as ours illustrate the difficulty of showing that lifetime fecundity is pollen limited. As noted by Janzen et al. (1980), orchids may have evolved under conditions of infrequent pollinator visits, so they may not be adapted to sustain high levels of fruit set. If this is true, unvisited flowers may serve primarily to attract pollinators. A single visit can be extremely effective in orchids because thousands of pollen grains are packaged in each pollinium.

The cost of reproduction may be relatively high in *Tipularia* because the reddish brown reproductive structures carry on little or no photosynthesis. However, sexual reproduction also entails a cost in other orchids with a variety of habits and phenologies. In two tropical species with photosynthetic reproductive organs, fruit set led to a decrease in future leaf area and flower production (Montalvo and Ackerman 1987, Zimmerman and Aide 1989). Similar responses were seen in winter-deciduous lady's slipper (Cochran 1986, R. Primack and P. Hall, *personal communication*). Lady's slipper orchids produce a single large fruit, which can result in an 8-14% decrease in leaf area the following year (R. Primack and P. Hall, *personal communication*). This cost of fruit set is remarkably similar to that found in *Tipularia*. Naturally pollinated *Tipularia* individuals produced ≈ 7 fruits per plant, resulting in a 14% decrease in leaf area the next year. In the

tropical orchid *Encyclia krugii*, fruit set had no effect on future growth, but fruit set was quite low (<4% of the flowers set fruit; Ackerman 1988). Aside from studies showing that fruit set often entails a cost in orchids, there are surprisingly few studies of the net cost of reproduction in other species. The generalization that reproduction is costly is probably valid,³ but further research on the relative costs of flowers, fruits, seeds, and their supporting organs will undoubtedly improve our understanding of how various life history traits evolve.

³ NOTE ADDED IN PROOF: This argument is contested in a recent (1988) paper by C. C. Horvitz and D. W. Schemske (Demographic cost of reproduction in a neotropical herb. *Ecology* 69:1741-1745).

ACKNOWLEDGMENTS

We thank Jay O'Neill, Lisa Balduman, and Elizabeth English for field assistance; and James Ackerman, Robert Efrid, Richard Primack, and Jess Zimmerman for providing unpublished manuscripts. The manuscript was improved by helpful comments from Robert Efrid, Candace Galen, Peter Curtis, Richard Primack, Maureen Stanton, Jay O'Neill, and our anonymous reviewers. This research was supported by a Smithsonian Postdoctoral Fellowship to A. A. Snow, the Smithsonian Environmental Sciences Program, and the Smithsonian Work-Learn Internship Program.

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