

# THE DYNAMICS OF FLOWERING AND FRUIT PRODUCTION IN TWO EASTERN NORTH AMERICAN TERRESTRIAL ORCHIDS, *TIPULARIA DISCOLOR* AND *LIPARIS LILIFOLIA*

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## Abstract

*Liparis lilifolia* (L.) Richard and *Tipularia discolor* (Pursh) Nutall. are common terrestrial orchids in deciduous forests of eastern North America. Although the species have different breeding systems, fruit production in both species is pollinator limited. *Liparis* is self-incompatible while *Tipularia* is self-compatible but anther cap retention promotes outcrossing. Annual variation in the number of plants in flower does not appear to be related to any easily identifiable climatological variable. The number of flowers per inflorescence does not vary greatly in either species. Observed differences in flowering and fruiting are most likely influenced by historical events at the individual level, especially costs associated with sexual reproduction and leaf herbivory. Results from these studies demonstrate the importance of long-term observations to understanding variations in patterns of reproduction of terrestrial orchid species.

## Introduction

Detailed information of breeding systems of North American terrestrial orchids exists for less than 40% of the known species (Catling and Catling 1990). Information on patterns of flowering and fruiting are incomplete because there have been few long-term studies of North American terrestrial orchids (Calvo 1990, Curtis and Green 1953; Firmage and Cole 1988; Gill 1989; Gregg 1989 and this volume; Light and MacConail this volume; Mehrhoff 1989; Whigham and O'Neill 1989). Even less is known about factors which control flowering and fruiting. In this paper we describe breeding systems and examine patterns of flowering and fruiting for two North American terrestrial orchid species, *Liparis lilifolia* (L.) Richard and *Tipularia discolor* (Pursh) Nutall. For *Tipularia*, we also consider the costs associated with flowering and fruiting and the influence that herbivory can have on growth.

## Species descriptions

*Liparis* is reportedly rare in mature forests but may become abundant after logging or other disturbances (Curtis and Green 1953; Niemann 1986; Sheviak 1974). It grows loosely imbedded in the litter layer and winters as a rootless corm at or near the soil surface. Each spring, new roots develop from the overwintering corm and each plant usually produces two basal leaves. Flowering occurs in late spring (Fig. 1).

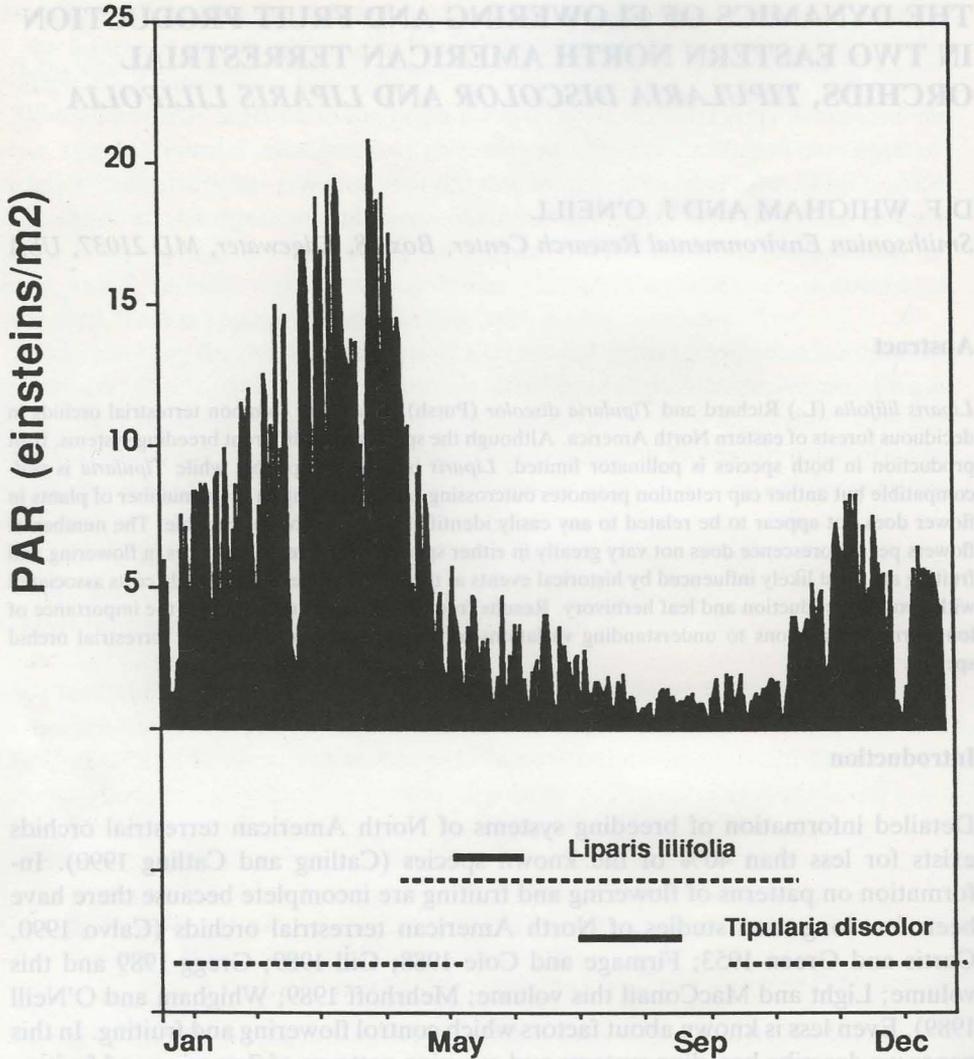


Fig. 1. Phenological pattern of *Liparis lilifolia* and *Tipularia discolor*. The periods of time when leaves are present and during which flowering occurs are shown in the dashed and solid lines respectively at the bottom of the figure. The top of the figure shows the amount of light measured 2 m above the ground in a deciduous forest at SERC. Data were compiled with a Cambell CR-21 micrologger using LI-COR quantum sensors.

By autumn senescence, the parent corm of each plant has completely disappeared and has been replaced by a new corm. Asexual reproduction is possible through the production of offsets. Floral characteristics have been described by Correll (1978).

*Tipularia* is common in both mature and successional deciduous forests. It has a different phenology and growth pattern than *Liparis* (Fig. 1). Individuals normally

produce one leaf and underground corm per year. Leaves are present from early autumn to early summer and flowering occurs in the middle of the summer (July–August) after leaf senescence (Fig. 1). Corms are normally shallow rooted and persist for several seasons so that the belowground component of any individual includes corms of several ages. Asexual reproduction in *Tipularia* usually follows sexual reproduction. Flowering plants will often produce a second leaf which results in two axes of growth. The two axes separate when the corm that forms their common connection senesces. Patterns of growth and nutrient cycling in *Tipularia* can be found in Whigham (1984).

### Breeding systems

There appears to be a wide range of breeding patterns in North American terrestrial orchids. Most species produce fruits when flowers are self-pollinated (Table 1) but autogamy is rare as few species have evolved mechanisms for selfing to occur (Mehrhoff 1983; Catling 1983; Catling and Catling 1990). There appears, however, to be variation in the degree of intraspecific self-compatibility as shown for *Calopogon tuberosus* and *Galearis spectabilis* in Table 1.

*Liparis* is one of the few species (Catling 1983; Gregg 1989) that is not self-compatible and the success of cross-pollinations depends on the proximity of the pollen recipient to the donor. In 1987, random exchange of pollen among plants within an area of approximately 400 m<sup>2</sup> resulted in 29.4% fruit set (Table 2). In 1988 we pollinated flowers with either pollen from their closest neighbour or with pollen from plants at a site located approximately 1 Km away. Flowers that received pollen from their nearest neighbour produced no fruit compared to 62.8% for inter-site pollinations. Lack of fruit set in nearest neighbour pollinations was probably due to incompatibility between asexually produced individuals that were genetically very similar.

The pollination ecology of *Tipularia* has been described by Whigham and McWethy (1980) and will only be summarized here. Plants are pollinated by moths and successful fruit set can occur as a result of both intra- and inter-inflorescence crosses. Like most terrestrial orchids, fruit set in *Tipularia* appears to be pollinator limited (Snow and Whigham 1989). Fruits develop from self-pollinated flowers (Whigham and McWethy 1980) although autogamy is unlikely as outcrossing is promoted by anther cap retention (Catling and Catling 1990).

Fruit set in most terrestrial orchids appears to be pollinator limited and there is wide diversity in whether or not species offer rewards to pollinators and how much reward is offered (Table 1). As many as 1/3 of the known orchid species appear to offer no floral rewards and depend on deception for pollination (Gill 1989). Although *Liparis* lacks nectar spurs and we have observed no obvious nectar, ants observed foraging on the lip suggests there may be some floral reward. Minute quantities of nectar produced on the lip surface of *Listera cordata* has been reported by Ackerman and Mesler (1979). *Tipularia*, on the other hand, offers nectar to

Table 1. Summary of breeding system studies of North American terrestrial orchids. FS = % open pollinated flowers producing fruits. Aut = Autogamy, Self = Self-compatible when hand pollinated and given as % of flowers which matured fruits or observations (Yes or No) if selfing produced fruits. N = the presence of nectar and F = the presence of a fragrance. Instances where there was doubt about the presence of a fragrance are indicated with a ?. A dash line (-) indicates that data were not reported and P., under Species, is the abbreviation for *Platanthera*.

Species	FS	Aut	Self	Rewards	Author(s)
<i>Aplectrum hyemale</i>	82	Yes	-	None	Hogan 1983
<i>Arethusa bulbosa</i>	5	-	Yes	N,F	Thien and Marcks 1972
<i>Calopogon tuberosus</i>	12-40	No	87%	None	Firmage and Cole 1984
<i>Calopogon tuberosus</i>	16	-	No	None	Thien and Marcks 1972
<i>Cleistes divaricata</i>	20-75	No	100%	F?	Gregg 1989
<i>Cyclopogon cranichoides</i>	26-61	No	97%	None	Calvo 1990
<i>Cypripedium acaule</i>	2	Yes	19%	None	Gill 1989
<i>Cypripedium acaule</i>	1.7	Yes	90-100%	100	Primack and Hall 1990
<i>Isotria medeoloides</i>	83	Yes	-	No	Mehrhoff 1983
<i>Isotria verticillata</i>	21	No	95%	F	Mehrhoff 1983
<i>Liparis lilifolia</i>	0-7.3	No	No	N?	This study
<i>Listera cordata</i>	61-78	No	Yes	N,F	Ackerman and Mesler 1979
<i>Galearis spectabilis</i>	9-11	No	4%	N	Dieringer 1982
<i>Galearis spectabilis</i>	53.5	No	65.4%	N	Zimmerman (Pers. comm.)
<i>P. blephariglottis</i>	62.4	No	90.9%	N,F?	Cole and Firmage 1984
<i>P. blephariglottis</i>	23-25	No	100%	N	Smith and Snow 1976
<i>P. ciliaris</i>	-	No	-	N	Smith and Snow 1976
<i>P. ciliaris</i>	84-87	No	91%	N	Robertson and Wyatt 1990
<i>P. ciliaris</i>	65-67	No	79%	N	Robertson and Wyatt 1990
<i>Pogonia ophioglossoides</i>	10-100	-	Yes	N,F	Thien and Marcks 1972
<i>Tipularia discolor</i>	0-38	No	Yes	N	Whigham and McWethy 1980

potential pollinators and pollinator activity within an inflorescence is related to the distribution and amount of nectar present (Whigham and McWethy 1980).

Table 2. Results of breeding experiments on *Liparis lilifolia*. Control plants were open pollinated. Augmented flowers were hand pollinated with pollen from nearest neighbours, from same site (intra-site) or from a site (inter-site) 1 Km away. Plants were caged after hand-pollinations were made. N is the number of flowers crossed or the number available for pollination (Control plants).

Year	Treatment	Pollen source	N	% fruit set
1987	Control	open	353	2.5
	Augmented	intra-site	109	29.4
1988	Control	open	453	0.7
	Augmented	nearest neighbour	29	0.0
	Augmented	inter-site	43	62.8

## Patterns of flowering and fruit set

### *Liparis*

#### Methods

*Liparis* has been studied at three sites in deciduous forests at the Smithsonian Environmental Research Center (SERC), located on the Rhode River watershed (Correll 1977) approximately 12 Km south of Annapolis, MD. We only present data from Site 1 because of the small number of plants at the other sites and because similar patterns have been observed at all sites. Site 1 is located in a 4 ha second growth forest that was in alfalfa cultivation in 1938 (D. Higman personal communication) and aerial photographs indicate that the forest had not developed as late as 1957. The forest is currently dominated by *Liquidambar styraciflua*, *Prunus serotina*, and *Liriodendron tulipifera* with an understory dominated by vines, primarily *Rhus radicans* and *Lonicera japonica*. Plants at all sites are found as solitary individuals or groups of up to a dozen independent plants. All plants were marked and have been censused annually for status (flowering, vegetative, absent). The number of flowers and fruits was recorded for sexually reproductive plants.

#### Results and discussion

Most *Liparis* at Site 1 flowered each year (Fig. 2). Similar to *Ophrys apifera* (Wells and Cox 1989), individuals appear to flower regularly once they reach a minimum critical size. The number of flowers per inflorescence varied little between years and the number of fruits produced has been consistently very low (Fig. 3), most likely due to the combined effects of pollinator limitations and self-incompatibility as described above. The number of individuals that were absent aboveground in any given year has been low except in 1990 when, for unknown reasons, almost half of all individuals produced no leaves. We do not know how many years *Liparis* can survive without producing leaves but our experience suggests that it is not more than one or two. Similar patterns (*i.e.*, plants absent for one to several years) have been found for other terrestrial orchid species (Calvo 1990; Hutchings 1987a, 1987b; Inge and Tamm 1988; Mehrhoff 1989; Willems 1982, 1989).

### *Tipularia*

#### Methods

We have monitored 34 groups of plants since the autumn of 1977 (Whigham 1984; Whigham and McWethy 1980; Whigham and O'Neill 1989). The groups are located in a deciduous forest at SERC similar to the 'tulip popular association' described by

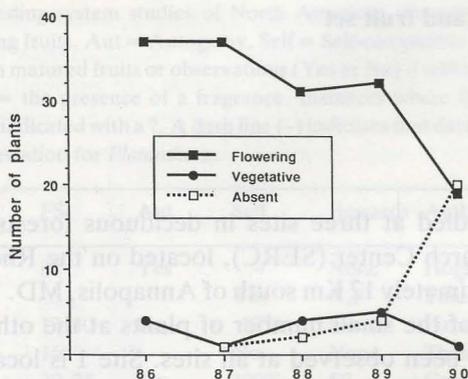


Fig. 2. *Liparis lilifolia* data from Site 1 showing annual changes in the number of plants with leaves, the number of flowering plants, and the number of absent plants, (i.e., no above ground leaf tissue present).

Brush *et al.* (1980). The stand now approximately 125 years old, originated from pasture abandoned after the Civil War (D. Higman, personal communication) and there has been no cutting on this parcel since at least 1915 (Parker *et al.* 1989). Individual plants are marked and leaf area has been calculated each year from linear measurements of leaves as described in Snow and Whigham (1989). The number of flowers and fruits per inflorescence was determined for sexually reproductive individuals. Flowers were counted during anthesis and fruits in late-August and again in late October.

### Results and discussion

Size appears to control flowering in *Tipularia* as individuals that flowered had significantly ( $P \leq 0.0001$ ) larger leaves than vegetative plants [flowering =  $24.5 \text{ cm}^2 \pm 0.9$  (1 SE); vegetative =  $13.9 \pm 0.3$ ]. Unlike *Liparis*, however, individuals that have reached reproductive size do not flower regularly as the number of plants

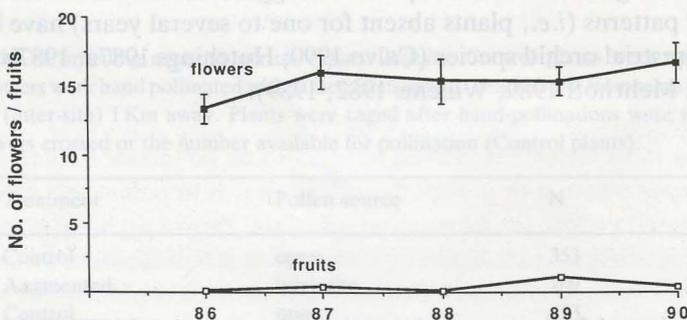


Fig. 3. Annual mean number of flowers and fruits per inflorescence ( $\pm 1$  standard error) for *Liparis lilifolia*.

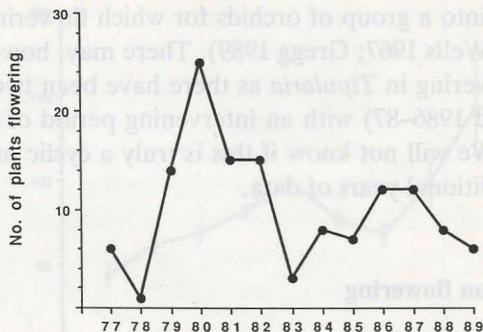


Fig. 4. Number of *Tipularia discolor* individuals flowering from 1977 to 1989.

flowering per year varied widely (Fig. 4). The number of times that individuals have flowered and the number of years between flowering events has also varied considerably. The largest number of individuals have never flowered or have only flowered once (Fig. 5a). For plants flowering two or more times, the majority flowered the next year or within the next two or three years (Fig. 5b). Data from other long-term studies of terrestrial orchids suggest that irregularity in flowering is more common (Cole and Firmage 1984; Farrell 1985; Firmage and Cole 1988; Hutchings 1987a; Inghe and Tamm 1988; Mehrhoff 1989; Tamm 1948, 1972; Wells 1967, 1981; Willems 1989) than regular flowering (Willems 1982; Wells 1967).

In addition to size, Wells and Cox (1989) suggested that flowering in *Ophrys apifera* was controlled by climatological conditions, particularly soil water availability. Firmage and Cole (1988) suggested that irregular flowering of *Calopogon tuberosus* was caused by variation in winter precipitation. Flowering of *Tipularia* has not been significantly related to either total annual precipitation or the amount of precipitation during different periods of time during the year (Table 3). *Tipularia*

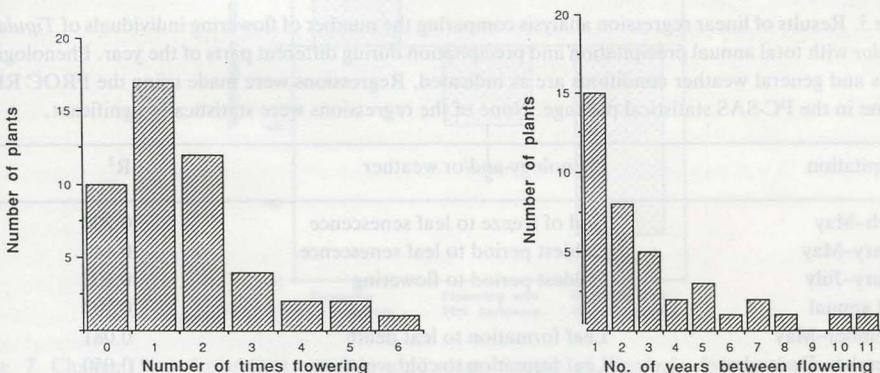


Fig. 5. Part A shows the number of individuals of *Tipularia discolor* that flowered between 0 and 6 times during the first 13 years of the study. Part B shows the frequency distribution for the number of years between flowering events for individuals that flowered two or more times.

thus appears to fall into a group of orchids for which flowering is controlled by a complex of factors (Wells 1967; Gregg 1989). There may, however, be a long term cyclic pattern of flowering in *Tipularia* as there have been two peaks in flowering activity (1979–82 and 1986–87) with an intervening period of 2–3 years with little flowering (Fig. 4). We will not know if this is truly a cyclic pattern until we have collected several additional years of data.

### Effects of herbivory on flowering

Herbivory and the energetic and nutritional costs associated with sexual reproduction undoubtedly influence future growth and reproduction. In some terrestrial orchids the high cost of reproduction has been proposed to be the reason that individuals do not appear above ground for one or more years following flowering (Hutchings 1987a). To date, however, there have been few quantitative assessments of those costs. Snow and Whigham (1989) showed for *Tipularia* that the size of belowground corms produced during the year following flowering was least in plants which produced high numbers of fruits. Plants with intermediate numbers of fruits produced intermediate sized corms compared to plants with no fruits and plants with large numbers of fruits. Similar results were reported by Primack and Hall (1990) for *Cypripedium acaule*; but see Calvo (1990) for contrasting results. Figure 6 shows the relationship between sexual reproduction and the area of individual leaves for *Tipularia*. Leaf area increased each year leading to the flowering event and then decreased with complete recovery after three years.

Herbivory can also influence individual plant performance. At our study site, individual plants experience frequent and complete leaf herbivory (Whigham and O'Neill 1989; Whigham 1990a). What are the combined impacts of sexual reproduction and herbivory? Evidence from a controlled defoliation experiment carried out

Table 3. Results of linear regression analysis comparing the number of flowering individuals of *Tipularia discolor* with total annual precipitation and precipitation during different parts of the year. Phenological stages and general weather conditions are as indicated. Regressions were made using the PROC REG routine in the PC-SAS statistical package. None of the regressions were statistically significant.

Precipitation	Phenology and/or weather	R <sup>2</sup>
March–May	End of freeze to leaf senescence	0.204
January–May	Coldest period to leaf senescence	0.149
January–July	Coldest period to flowering	0.105
Total annual		0.103
September–May	Leaf formation to leaf death	0.081
September–December	Leaf formation to cold weather	0.050
January–March	Coldest period to start of growing season of most woodland herbs	0.050
August–November	Flowering to first cold weather	0.008

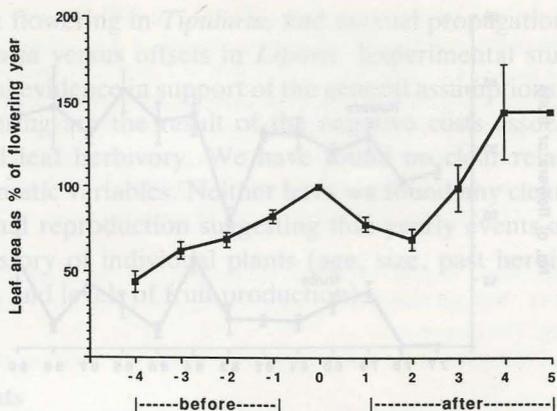


Fig. 6. Leaf area of *Tipularia discolor* before and after flowering as a percent of the leaf area during the flowering year (0 on the X-axis). Values are means  $\pm$  1 standard error. Data represent flowering individuals that had between 1 and 4-5 years before and/or after flowering without any leaf herbivory.

for three years (details can be found in Whigham 1990b), indicated that the change in total plant biomass from the year of flowering to the next year was significantly different ( $P \leq 0.001$ ) for plants that suffered no simulated herbivory compared to 50 and 100% defoliated plants which produced fruits (Fig. 7). The increase in biomass resulted from the second leaf and corm that was produced by most flowering plants.

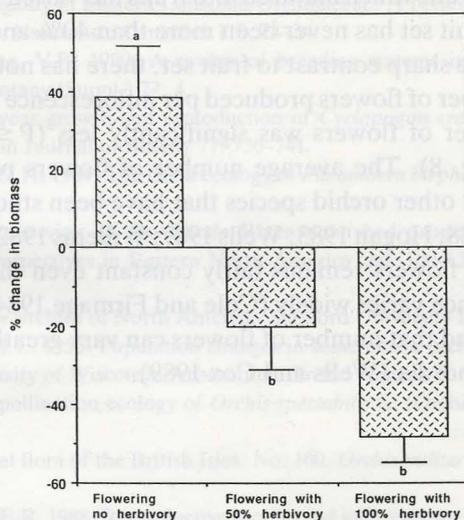


Fig. 7. Change ( $\% \pm 1$  standard error) in total plant biomass of *Tipularia discolor* from the year of flowering to the next year for individuals which: 1) flowered and suffered no herbivory, 2) flowered and had 50% of their leaf area removed, and 3) flowered and had 100% of their leaf area removed. Details of the leaf manipulation study can be found in Whigham (1990b). Means that are not significantly different share the same letter.

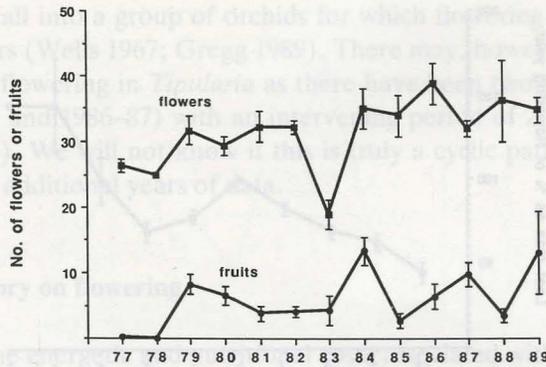


Fig. 8. Number ( $\pm 1$  standard error) of flowers and fruits per inflorescence for individuals of *Tipularia discolor* that flowered during the first 13 years of the study.

Branching of plants following flowering can thus offset the negative impacts of flowering on the area of individual leaves (Fig. 6 and Snow and Whigham 1989). Total biomass of plants which both flowered and had 50 or 100% herbivory, however, decreased dramatically. While the means were different (Fig. 7), the two groups were not significantly different from each other.

In *Tipularia*, there clearly is a high cost associated with the combined effects of herbivory and fruit production. Under natural conditions, however, the costs are most often kept to a minimum because of branching and fruit set is low (Fig. 8). While the number of fruits which matured into fruits has varied significantly between years ( $P \leq 0.0005$ ), fruit set has never been more than 40% and in most years it has been less than 20%. In sharp contrast to fruit set, there has not been any significant difference in the number of flowers produced per inflorescence with the exception of 1983 when the number of flowers was significantly less ( $P \leq 0.01$ ) due to inflorescence damage (Fig. 8). The average number of flowers per inflorescence was fairly constant in most other orchid species that have been studied for several years (Firmage and Cole 1988; Hogan 1983; Wells 1967; Willems 1982). In some instances, the modal number of flowers remains fairly constant even though the number of flowers per inflorescence varies widely (Cole and Firmage 1984). In contrast, Inghelbrecht and Tamm (1988) found that number of flowers can vary greatly, most likely due to abortion of floral primordia (Wells and Cox 1989).

## Conclusion

*Liparis* and *Tipularia* share characteristics that are common among terrestrial orchids. The number of flowers per inflorescence does not vary much from year to year but both species are pollinator limited and usually produce very few fruits. Dissimilarities include the types of breeding systems (self-incompatible in *Liparis* and self-compatible but obligate outcrossing in *Tipularia*), regular flowering in *Liparis*

versus infrequent flowering in *Tipularia*, and asexual propagation by 'death-from-behind' in *Tipularia* versus offsets in *Liparis*. Experimental studies of *Tipularia* provide additional evidence in support of the general assumptions that the irregular patterns in flowering are the result of the negative costs associated with sexual reproduction and leaf herbivory. We have found no clear relationship between flowering and climatic variables. Neither have we found any clear population level responses in sexual reproduction suggesting that yearly events are probably controlled by the history of individual plants (age, size, past herbivory events, past flowering events, and levels of fruit production).

### Acknowledgements

Financial support for the project has been provided by the Smithsonian Environmental Sciences Program. We thank Jess Zimmerman, Lisa Wagner, Tim Spira, and Zhigang Wang for their comments on the manuscript.

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**Abstract**

Examination of individual hermaphroditic bisexual flowers, in which pollen is dispersed in packets (i.e. pollinia), allows pollen import, export and the potential levels of self-pollination to be estimated. Flowers may be classified as belonging to a number of distinct classes depending on whether they are intact (i.e. no pollinia removal or insertion), or if pollinia have been removed and/or inserted. Examination of flowers of *Epipactis atrorubra* (L.) Crantz has established that pollinia export (male function) in this species is positively correlated with investment in secondary floral characteristics. In the present study the flowers of plants of *E. atrorubra*, *Anacamptis pyramidalis* (L.) Rich. and *Dactyloctenium aegyptium* (L.) Ventenat. were examined at three distinct field sites. Rates of pollen import and export differed considerably between species and within populations. For example, recorded mean rates of pollinia removal among plants of *D. aegyptium* ranged from approximately 7–23%. The lower value was obtained from plants in a wooded site, the higher value for plants from an open grassland. Within populations the performance of individual plants varied considerably, with rates of pollinia export and import ranging from 0 to 98 and 0 to 35% respectively. In all cases pollinia export exceeded pollinia import. No flowers were classified in which pollinia import occurred prior to pollinia export. Fruit set was also extremely variable. All three species were shown to be capable of autogamy. The extent of autogamy in plants of *E. atrorubra* was found to be negatively correlated with inflorescence length and flower number. The relationship between pollinia export and the extent of secondary floral investment differed between species. Among plants of *E. atrorubra* and *A. pyramidalis* pollinia export was related to inflorescence size. It is suggested that in these species secondary floral characteristics serve primarily to increase male fertility.

**Introduction**

In hermaphroditic plants male fertility or function is associated with the effective dissemination of pollen, while female fertility involves the receipt of pollen and the production of seeds (Bell 1985; Charlesworth 1989). It is clear that sexual asymmetry, non-equal male/female sex functioning (Ross 1990) and low female fertility occur frequently among hermaphroditic plants (Charlesworth 1989). When levels of resource allocation to pollen, ovule and seed production are considered, the in-