

OBSERVATIONS ON REPRODUCTION IN
TRIPHORA TRIANTHOPHORA (ORCHIDACEAE)

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ABSTRACT

A small population of the orchid *Triphora trianthophora* in western Massachusetts was investigated over a six-year period (1988 through 1993). Observations on the flowering habits and seed capsule production are described, as well as vegetative reproduction by means of tuberoids. *Triphora* produces an abundance of short-lived flowers yet very few capsules are initiated. The majority of *Triphora*'s existence is spent underground reproducing asexually by means of new tuberoids.

Key Words: *Triphora trianthophora*, orchid, tuberoids

INTRODUCTION

Triphora trianthophora is a small woodland orchid, elusive and secretive, appearing abundantly one year and rare or absent for many succeeding years (Lownes, 1920; Ames, 1948; Sheviak, 1974; Brackley, 1981). *Triphora trianthophora* also shows synchronous flowering, the majority of its short-lived flowers appear 48 hours after a temperature drop (Brackley, 1981; Keenan, 1986, 1988; Sheviak, 1974). In fact, all species of *Triphora* which are not self-pollinating exhibit gregarious flowering (Dressler, 1981) apparently to increase their chances of cross-pollination (Luer, 1975). Even so, *Triphora trianthophora* rarely sets seed (Lownes, 1920; Keenan, 1992).

The most unusual feature of this orchid, however, is its existence for years at a time in a subterranean, tuberous condition (Lownes, 1920; Ames, 1948; Zavitz and Gaiser, 1956). Although the tribe Triphoreae appears to be a relic group with no close allies, it does share a unique feature with members of the tribes Orchideae, Diseae and Diurideae in having these root-stem tuberoids (Dressler, 1981). I started observing the underground tuberoids of *Triphora* in part because of a statement made by Oakes Ames in 1948 in that he supposed there was a "... maximum size for the tubers that bear flowering stems." Every plant of *T. trianthophora* has from one to numerous tuberoids attached by stolons. These tuberoids are thickened underground storage structures superficially similar to tubers, but structurally different. As Dressler (1981) points out, true tubers are not found in orchids.

The primary tuberoid contains the apical bud which may form a new shoot in the growing season. Axillary buds form secondary tuberoids at the end of slender stolons. These secondary tuberoids continue to increase in size with the age of the plant, along with increasing length of the stolon. The stolon tends to grow downwards into the leaf litter so that with accumulating litter accounts for the depth of the primary tuberoids. These secondary tuberoids on becoming detached from the parent plant form primary tuberoids of new plants with the same genotype as the parent.

Most plants, however, do not form flowering shoots but remain in the leaf litter (pers. obs.), and these plants consist of primary and secondary tuberoids as seen in Figure 4a and 4b.

This paper presents the observations gathered over six years on: 1) sexual reproduction in *Triphora trianthophora*, in particular the reason for low capsule set; and 2) vegetative reproduction in *Triphora*, particularly the underground growth form with possible correlations to population fluctuations, and the relationship between primary tuberoid size and the plant's reproductive status.

METHODS

I became acquainted with *Triphora trianthophora* in 1988, when I began studies on a small population in western Massachusetts for the Massachusetts Natural Heritage and Endangered Species Program.

The study site comprises an area of approximately two acres of northern hardwood forest dominated by *Fagus grandifolia* and *Acer saccharum*. The site is on a southeast facing slope at an elevation of 900–1100 feet. It is midslope being approximately 300 feet above the Deerfield River basin.

The study area was subdivided into distinct sites where the plants were located. In 1988 there were 25 sites and in each succeeding year I found additional sites until there were a total of 72 sites in 1993, all within the general area. The cumulative total of vegetative and reproductive plants observed over the six year period was 1448.

I observed the plants on a daily basis for their entire above-ground existence of approximately one month, from their first emergence through the litter, to capsule set. Each site was monitored for the total number of plants; number of vegetative plants;

plants which produced buds but failed to blossom (in all cases this was due to some type of herbivory); plants which blossomed but did not initiate a seedpod; and plants which ripened seedpods. Percent capsule set was determined by the ratio of capsules set to total buds produced by the population.

While collecting data on each site, any pollinators or floral visitors were noted, and also whether the plants had undergone any type of herbivory.

A few plants that did not produce capsules were carefully removed from the litter and the length of their primary tuberoid was measured. This group included small primary tuberoids which had never produced any stem; tuberoids with hyaline stems (fragile, translucent stems remaining under the litter not producing leaves or flowers but with one or more secondary tuberoids attached); vegetative plants (those having above-ground stems with one small leaflet but no flowers); and plants with one, two, three, or four flowers.

As I started removing litter I also noted many other tuberoids in the same vicinity that had produced neither leafy nor flowering stems. These consisted of a primary tuberoid and one to many secondary tuberoids. Some had hyaline stems with secondary tuberoids but had never produced above-ground stems. Many large tuberoids were also noted which had previously produced above-ground stems but had not produced any in the current year. These tuberoids were not measured. Due to the invasive nature of measuring primary tuberoid length, only a small sample was measured each year.

A yearly comparison was made of the total number of plants for the original 25 sites as well as comparing fluctuations within individual sites.

RESULTS

Observations on Sexual Reproduction

Throughout the six-year study period, the majority of *Triphora trianthophora* plant produced flower-bearing stems; only 10% or less failed to flower in any given year. (Figure 1). Most of the plants bore one or two flowers; those having three or four were much less frequent totaling less than 10% in any given year. This pattern remained relatively constant over six years.

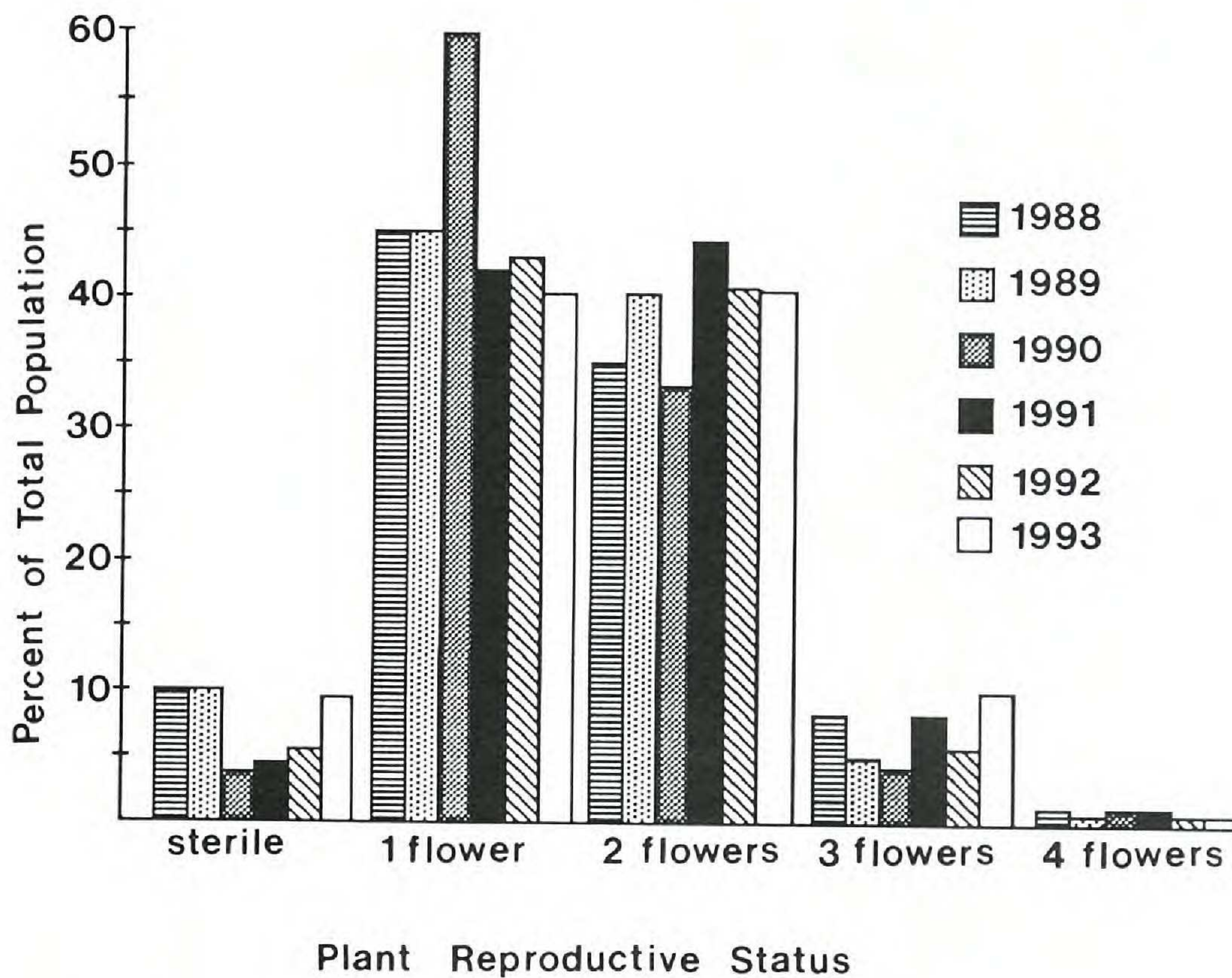


Figure 1. Percentages of plants of differing reproductive status in a *Triphora* population over a six-year period.

Figure 2 illustrates on a yearly basis the percentages of bud loss, flowers produced and capsules ripened out of the total bud population.

The large percentage of buds lost was caused by several factors. Rarely, a few buds would be underdeveloped and tiny and these would always drop off prior to flowering. Occasionally, entire plants had been consumed by chipmunks (their tunnels were found under clumps of *Triphora* plants) and no trace of plant or tuberoids could be found. Slugs were the most destructive herbivores of *Triphora*. Stems were chewed through, usually at litter level, and the plants would be lying on the ground. Sometimes, they were chewed in half higher up and occasionally the buds were half eaten. I noted slugs in the upper litter layers many times and observed slugs on *Triphora* plants (including the tuberoids) several times.

Also illustrated in Figure 2 is that capsule production relative to total buds produced is very low. However, out of 110 capsules

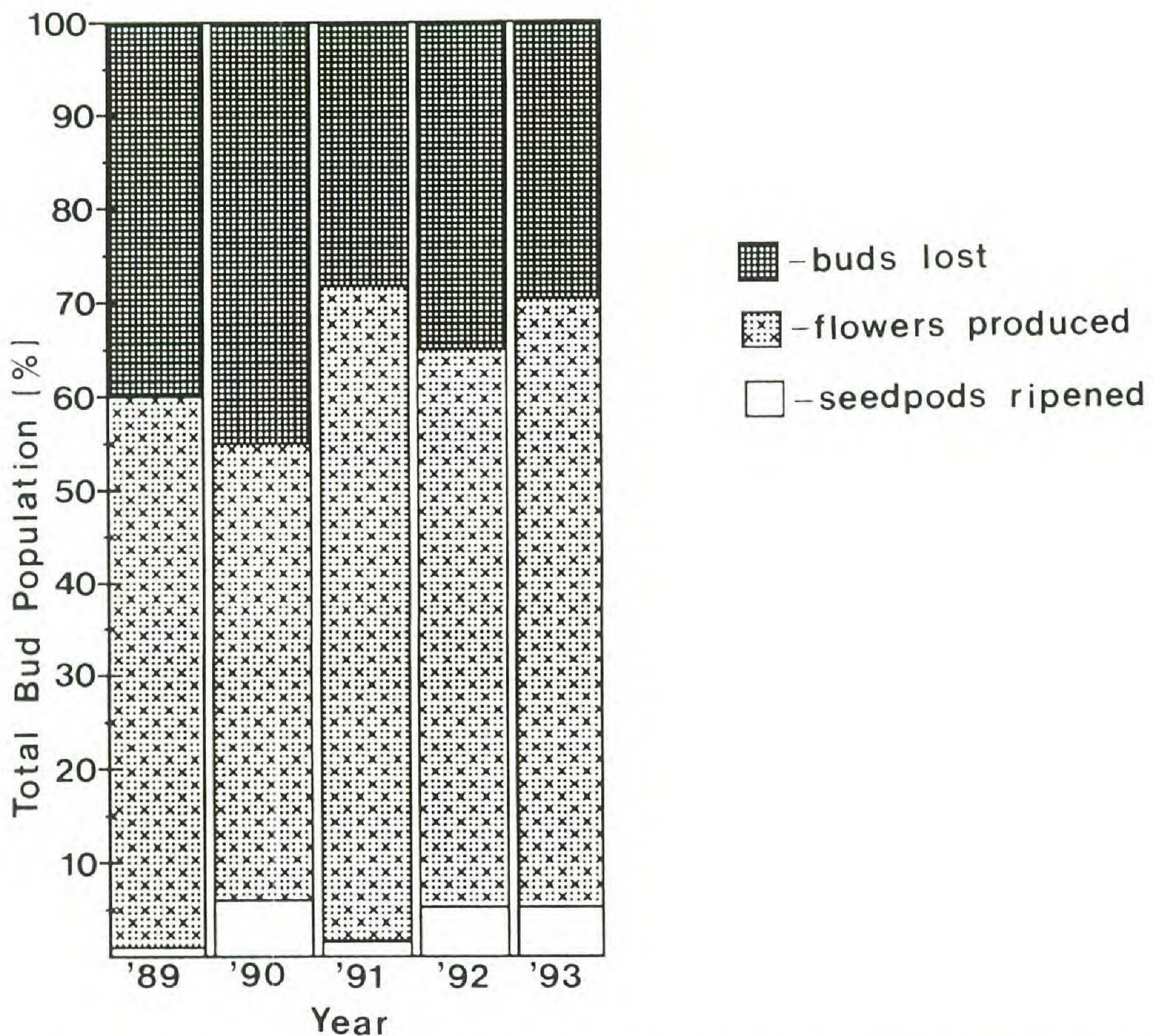


Figure 2. Percentages of buds lost, flowers produced and seedpods ripened out of the total bud population, compared yearly.

initiated 104 ripened, which is 95%. The other 6 did not ripen because of loss of the plant due to herbivory.

It appears that few of the flowers are actually pollinated, supported by the fact that on only two occasions in six years did I note any floral visitors. One appeared to be a small species of bumblebee (*Bombus*) which entered the blossom for a few seconds, then backed out with pollinia attached. The only other flower visitor I observed was a much smaller and slender bee probably belonging to the genus *Hylaeus*. I did not observe any pollinia removal with its visit, but whether the bee was too small or the pollinia had already been removed could not be determined.

Another factor contributing to low capsule set is the fact that the *Triphora* blossom is available to pollinators for one day only. The day following a bloom shows noticeable fading and drooping

Table 1. One-way analysis of variance of reproductive status. The length data were log transformed to homogenize the variance and the log of length was then used as the dependant variable.

Source	Analysis of Variance				
	Sum-of-Squares	df	Mean-Square	F-Ratio	P
Reproductive status	29.766019	5	5.953204	47.560594	0.000000
Error	8.511623	68	0.125171		

tuberoid with no shoot development had the smallest primary tuberoids; those plants with either hyaline stems or sterile leaflets had slightly larger primary tuberoids; and primary tuberoid size tended to increase with increasing numbers of flowers per plant. A one-way ANOVA was done on the data with the log of length as the dependent variable. The length data were log transformed in order to homogenize the variances. As seen from the ANOVA table (Table 1), the developmental classes showed significant variation in tuberoid length. In order to analyze the variation between classes, a Bonferroni Adjustment was done. The results (shown by the letters in Figure 3) indicated which classes varied significantly from which other class.

The primary tuberoid is generally the largest and the deepest down in the litter from which the flowering stem and secondary tuberoids arise (*see* Figure 4). The secondary tuberoid closest to the primary tuberoid is the largest with smaller tuberoids appearing up the stem. There are many variations in the number of secondary tuberoids and their arrangement on any individual plant. Some plants have only one secondary tuberoid, in others I have counted up to 17. However, all plants have at least one. Occasionally the secondary tuberoids get quite large before becoming separated from the main plant. Several secondary tuberoids were even slightly larger than the primary tuberoid. There doesn't appear to be a specific size when the stolon disintegrates between the main plant and the secondary tuberoids. More likely, they separate as a result of physical forces since they are fragile and near the litter surface. The tuberoids remain in the leaf litter never reaching into the soil substrate.

Another distinct difference between primary and secondary tuberoids is that the primary tuberoid is a tan color whereas all secondary tuberoids are waxy white. I found tiny primary tuber-

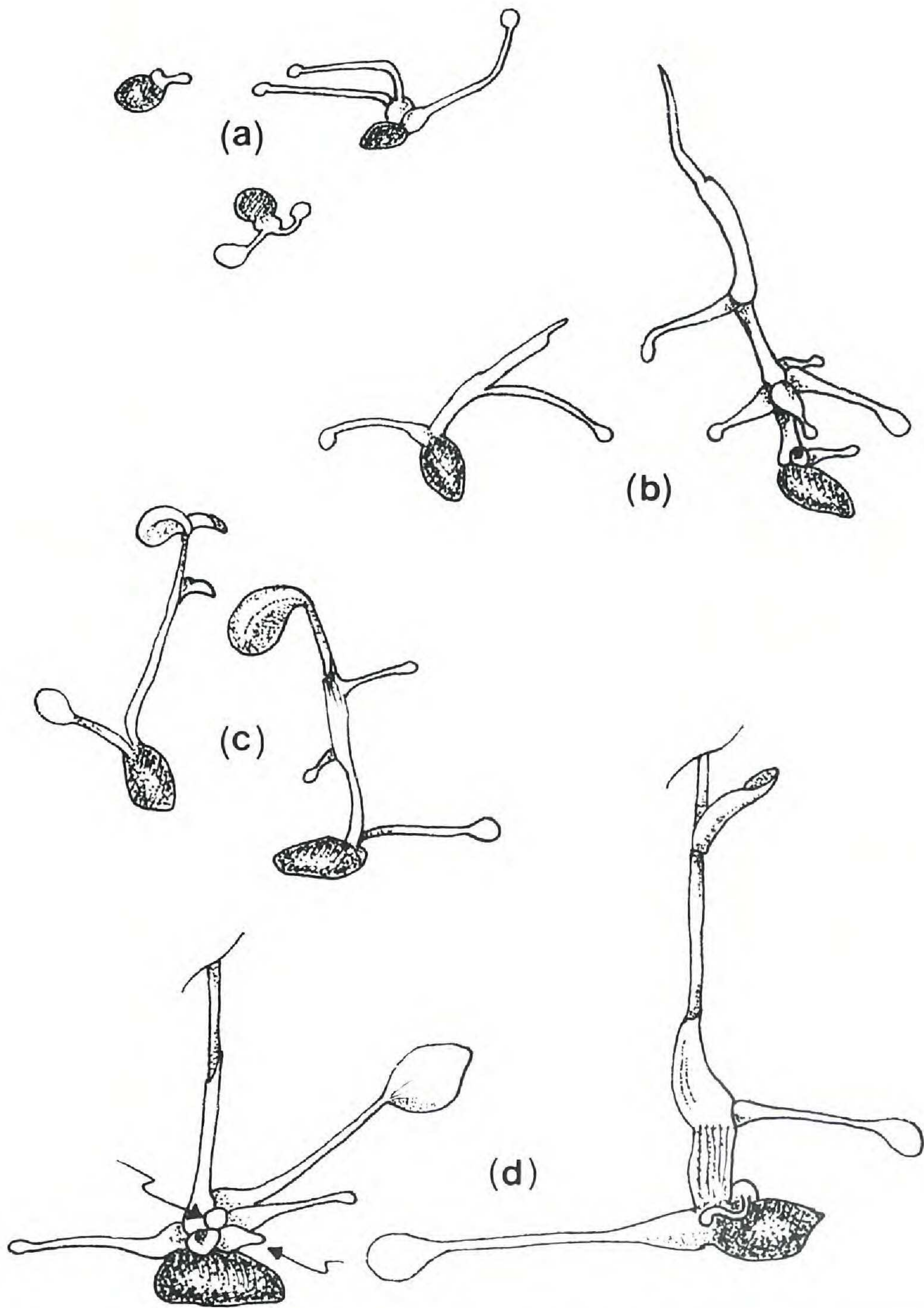


Figure 4. Variation in primary and secondary tuberoid growth in successive stages of *Triphora* development. (a) small primary tuberoids with secondary tuberoid development but no stem development; (b) hyaline stem production; (c) leaflet of a non-flowering shoot; (d) flowering plants (arrows show swellings near primary tuberoid which will develop into secondary tuberoids).

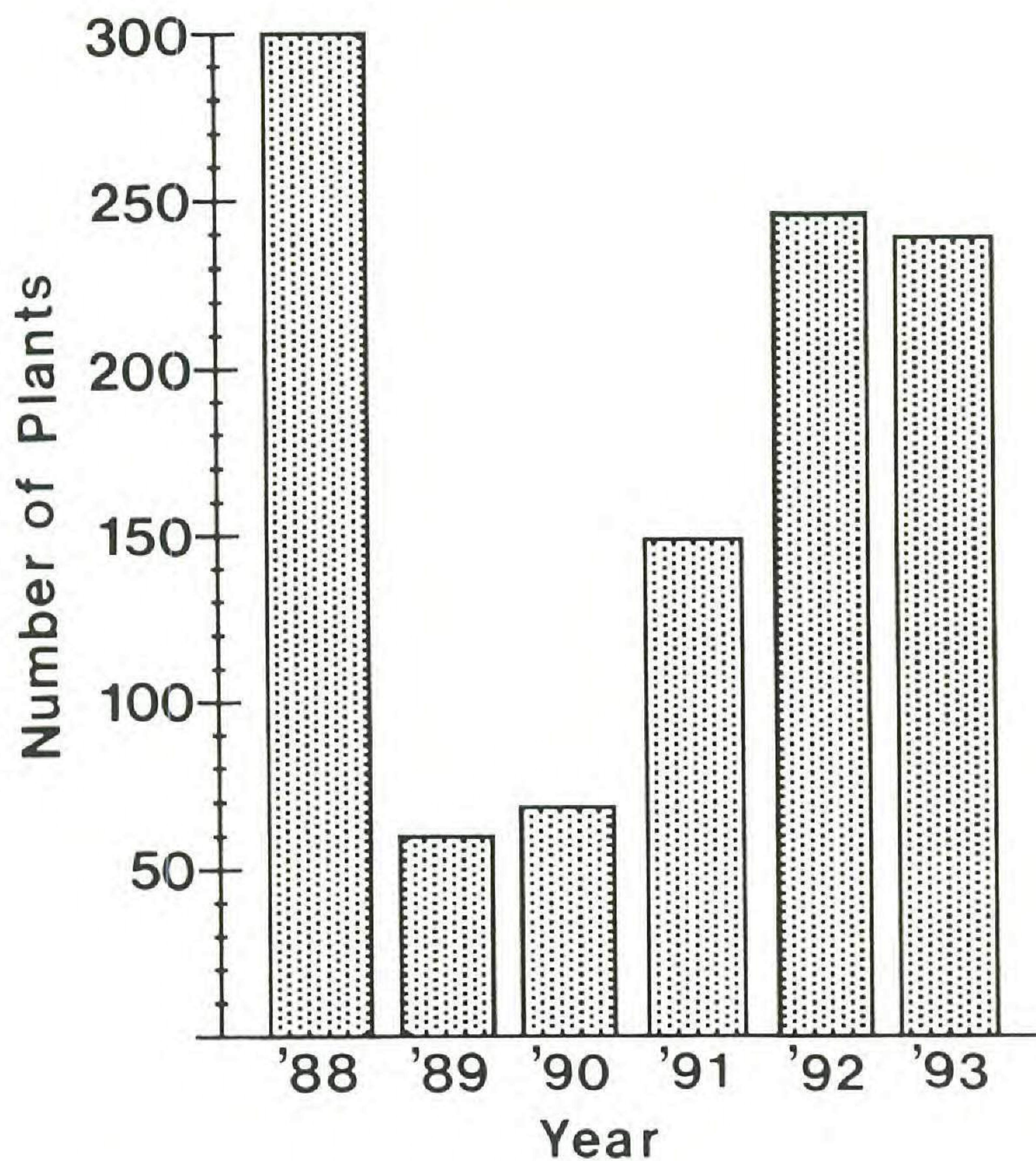


Figure 5. Fluctuations in the total population from 1988 through 1993 on the original 25 sites.

oids in the litter only 1 mm long, some of which were already producing a new secondary tuberoid.

Figure 5 shows the yearly fluctuations in population size for the original 25 sites found in 1988. It suggests a pattern of increasing and decreasing population size, but more data is needed to confirm this.

Table 2 shows the fluctuations of plants within each of the 25 sites over the six years. There is not only a great deal of variation in plant numbers between sites but also within individual sites on a year-to-year basis. What the Table doesn't show is that plants that reappear are not always in the same location as in previous years even though they are in the same site. This indicates that there are many primary tuberoids existing in the litter without producing shoots for years at a time.

Due to this sporadic shoot production, it is very difficult to assess population size and vigor. Their absence for many years does not mean they are not there. I confirmed this by removing

Table 2. Actual numbers of vegetative and flowering plants for each of the original 25 sites and their yearly fluctuations.

Site #	Total Number of Plants					
	1988	1989	1990	1991	1992	1993
1	4	0	0	0	0	0
2	8	0	6	4	9	11
3	4	0	0	0	0	1
4	3	0	0	0	0	0
5	7	0	2	2	0	0
6	8	2	1	5	0	1
7	1	0	0	1	0	13
8	There is no site #8					
9	14	2	0	8	5	2
10	10	0	0	6	2	0
11	28	1	4	2	11	10
12	1	0	0	0	0	0
13	2	1	0	0	0	0
14	3	0	0	0	2	0
15	11	2	0	0	0	0
16	19	5	7	9	20	18
17	13	0	1	2	8	14
18	20	3	0	22	35	36
19	22	7	1	4	2	3
20	23	4	6	18	19	8
21	37	21	30	61	113	93
22	47	0	4	1	3	19
23	7	0	2	2	3	6
24	5	1	0	1	0	0
25	3	2	1	0	11	5
Total	300	51	65	148	243	240

litter in several potential sites in 1989 where I had never observed *Triphora*. In three of the sites I found numerous tubers and in 1990 these areas contained 21 flowering plants.

DISCUSSION

Triphora trianthophora is a species of the climax hardwood forest always associated with *Fagus grandifolia* (Lownes, 1920; Zavitz and Gaiser, 1956; Sheviak, 1974; Crow and Stokes, 1980; Brackley, 1981; Martin, 1983; Keenan, 1992). It initiates shoot growth and flowers in August when the herbaceous environment under a full canopy is characterized by very low light levels,

highest soil temperatures, and lowest nutrient and water availability due mainly to uptake by trees (Mahall and Bormann, 1978). Many of the ground herbs here are spring ephemerals which complete their life cycles prior to canopy closure. Early leaf and flower production may be the result of selection for completing these processes while light intensity at the forest floor is high and could be viewed as a method by which plants reduce interspecific competition (Newell and Tramer, 1978).

It has also been shown that spring ephemerals lack the capacity to modulate their photosynthetic and respiratory physiology in response to decreased light levels accompanying canopy closure. This lack of adaptability limits the ephemerals from exploiting reduced light environments and consequently ephemerals revert to a dormant condition soon after the canopy species leaf out (Chabot and Mooney, 1985).

Shade tolerant species such as *Triphora* carry out most of their growth and photosynthesis under a closed canopy. *Triphora* may be successful in this stressful habitat because its mycorrhizal association meets its energy and nutrient needs making it an obligate mycotroph for most of its existence. As a result, its leaves are reduced (indicating reduced photosynthetic capability), and much of its existence is spent beneath the leaf litter reproducing by means of new tuberoids. Many of *Triphora*'s associates are also saprophytic or root parasites. *Epifagus virginiana* is especially abundant. *Coralorrhiza maculata*, and *Monotropa uniflora* are also found thinly scattered in the herb layer.

Because of the positive correlation with *Fagus grandifolia*, it seems probable that there is a three-way connection from *Triphora* through its mycorrhizae to the *Fagus* roots and that *Triphora* may be indirectly receiving its nutrients and photosynthate from the beech trees. A similar situation occurs in the Australian orchid *Gastrodia cunninghamii* which lives almost entirely underground. Its tubers are covered with a network of fungal mycelia which penetrates the living roots of an adjacent tree, most often *Nothofagus* (Withner, 1974). This three-way relationship is known to occur in other orchids and plants (Harley, 1982; Harley and Harley, 1987; Bernhardt, 1989).

Although sample size for tuberoid measurements was small due to the invasive nature of sampling, analysis of the data indicates that the plant's reproductive status depends in part on primary tuberoid size. Since the variability in primary tuberoid size was quite large for 1 to 4 flowered plants and the fact that many

primary tuberoids of flowering size (i.e., greater than .7 cm) were discovered in the litter near measured plants suggests that *Triphora* continues a productive life under the litter reproducing vegetatively after it has produced a flowering shoot. Additional data may show that a primary tuberoid may produce many flowering shoots years apart.

It is not unusual for deciduous forest herbs to reproduce vegetatively as well as by seed. However, even for species that replace themselves primarily vegetatively, seeds are necessary for the establishment of new populations and nearly all species flower (Bierzychudek, 1982). The number of seedpods actually formed relative to the number of flowers produced may be largely controlled by pollinator activity and by general environmental and physiological conditions (Withner, 1974). This limitation of reproductive output by pollinators seems to be a common phenomenon in many species (Bierzychudek, 1981).

From personal observations, the woods in August have few pollinating insects. In order to ensure pollination, many of *Triphora*'s associates remain in flower for an extended time, such as *Solidago caesia*, *Aster divaricatus*, and *Laportea canadensis*. *Impatiens pallida* flowers continually throughout the summer with the later flowers being cleistogamous. *Epifagus virginiana*, an abundant saprophyte in the area, has sterile upper flowers, but abundantly fertile cleistogamous lower flowers.

Two other members of the Orchidaceae found scattered over the site include *Epipactis helleborine* and *Corallorhiza maculata*. These both share the feature of long flower availability to pollinators by successive opening of long-lived flowers. *Triphora*, on the other hand, only opens its flowers for one day, and that fact coupled with low pollinator availability accounts for the low capsule set. To offset the short duration of flower availability, however, *Triphora* flowers gregariously, i.e., many flowers open on the same day. Gregarious flowering is obviously an advantage to plants with short-lived flowers, as it gives a much greater chance of pollination than would be the case if the flowers opened sporadically over a long period (Lawson, 1966). These massed floral displays presumably increase the attractiveness to pollinators and in *Isotria verticillata*, the larger clones did have higher pollination percentages (Merhoff, 1983).

Triphora trianthophora appears well adapted to the habitat in which it is found. Since pollination and seed ripening occur rarely, *Triphora* utilizes vegetative propagation by secondary tuberoids

to ensure future generations in the extant population. This type of adaptation, however, may result in a loss of genetic variability in the population, and can become detrimental in that *Triphora trianthophora*, like many other plants, is sensitive to changes in its habitat. Loss of its habitat would mean certain destruction for an entire population. The fact that it may not be detected for years at a time makes this unique orchid especially difficult to protect.

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LITERATURE CITED

- AMES, O. 1948. Orchids in Retrospect: A Collection of Essays on the Orchidaceae. Botanical Museum of Harvard University, Cambridge, MA.
- BERNHARDT, P. 1989. Wiley Violets and Underground Orchids. Random House, Inc., NY.
- BIERZYCHUDEK, P. 1981. Pollinator limitation of plant reproductive effort. *Amer. Naturalist* 117: 838–840.
- BIERZYCHUDEK, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytol.* 90: 757–776.
- BRACKLEY, F. 1981. Orchids of New Hampshire. M.S. thesis, University of New Hampshire, Durham, NH.
- CHABOT, B. F. and H. A. MOONEY. 1985. *Physiological Ecology of North American Plant Communities*. Chapman and Hall, New York.
- CROW, G. AND I. STOKES. 1980. Rare and endangered plants of New Hampshire: a phytogeographical viewpoint. *Rhodora* 82: 173–189.
- DRESSLER, R. 1981. *The Orchids: Natural History & Classification*. Harvard University Press, Cambridge, MA.
- HADLEY, G. 1982. Orchid Mycorrhiza, pp. 85–118. *In*: J. Arditti, Ed., *Orchid Biology, Reviews and Perspectives*, Vol. II. Cornell University Press, London.
- HARLEY, J. L. AND E. L. HARLEY. 1987. A Check-List of Mycorrhiza in the British Flora. *New Phytol.* 105: 1–102.
- KEENAN, P. E. 1986. New stations for *Platanthera flava* and *Triphora trianthophora* and other observations. *Rhodora* 88: 411–412.
- . 1988. Three-birds orchids at Golden Pond. *Amer. Orchid Soc. Bull.* 57: 25–27.
- . 1992. A new form of *Triphora trianthophora* (Swartz) Rydberg, and Part

- 3 of observations on the ecology of *Triphora trianthophora* (Orchidaceae) in New Hampshire. *Rhodora* 94: 38–41.
- LAWSON, G. W. 1966. *Plant Life in West Africa*. Oxford University Press, London.
- LOWNES, A. E. 1920. Notes on *Pogonia trianthophora*. *Rhodora* 22: 53–55.
- LUER, C. A. 1975. *The Native Orchids of the United States and Canada*. New York Botanical Garden, NY. 361 pp.
- MAHALL, B. E., AND F. H. BORMANN. 1978. A quantitative description of the vegetative phenology of herbs in a northern hardwood forest. *Bot. Gaz. (Crawfordsville)* 139: 467–481.
- MARTIN, L. 1983. *Nodding Pogonia*. Maine State Planning Office. Pamphlet. Critical Areas Program.
- MERHOFF, L. A. 1983. Pollination in the genus *Isotria* (Orchidaceae). *Amer. J. Bot.* 70: 1444–1453.
- NEWELL, S. J. AND E. J. TRAMER. 1978. Reproductive strategies in herbaceous plant communities during succession. *Ecology* 59: 228–234.
- SHEVIK, C. J. 1974. An Introduction to the Ecology of the Illinois Orchidaceae. *Scientific Papers XIV*, Illinois State Museum, Springfield, IL, pp. 49–50.
- WITHNER, C. 1974. *The Orchids*. John Wiley & Sons, New York.
- ZAVITZ, C. H. AND L. GAISER. 1956. Notes on *Triphora trianthophora* in Ontario. *Rhodora* 59: 31–35.

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