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THE RELATIONSHIP BETWEEN AGE, SIZE, AND REPRODUCTION IN *TRILLIUM GRANDIFLORUM* (LILIACEAE)¹

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The relative importance of age and size as predictors of demographic parameters such as survivorship or reproductive status is generally unknown for herbaceous perennials, due primarily to the difficulty in estimating the age of herbaceous plants. We investigated the relationship between age, size, and reproductive status in *Trillium grandiflorum*, a rhizomatous perennial herb in which age can be estimated. We measured the leaf area and rhizome volume and estimated the age of plants in a study population that included reproductive and nonreproductive individuals. Reproductive plants were significantly older ($\bar{X} = 22.8$ years) than nonreproductive plants ($\bar{X} = 13.3$ years). Reproductive plants also had significantly larger total leaf areas and rhizome volumes. Total leaf area, rhizome volume, and age were positively correlated in both groups. Reproduction in this population occurred once plants reached a threshold leaf area or rhizome volume. Both measures of plant size, i.e., total leaf area and rhizome volume, were better predictors of plant reproductive status than was plant age.

Numerous studies of annual, biennial, and monocarpic perennial plants suggest that plant size is frequently a better predictor than plant age of important demographic parameters such as survivorship, onset of reproduction, and fecundity (e.g., Werner, 1975; Werner and Caswell, 1977; Baskin and Baskin, 1979; Meijden and Waals-Kooi, 1979; Gross, 1981; Hirose and Kachi, 1982; Young, 1985; Klinkhamer, de Jong, and Meelis, 1987). However, studies relating both age and size to survivorship and reproduction in polycarpic plants are fewer and come exclusively from work with woody species (e.g., Meyer, 1930, 1938). Since reasonable estimates of age from herbaceous perennials are difficult to obtain, investigations of the relationship among size, age, and demographic stage of herbaceous perennials are almost absent from the literature.

Before beginning reproduction, many polycarpic perennial herbs have a juvenile period of at least several years (Bierzychudek, 1982a). Although the onset of reproduction is a very important demographic characteristic of herbaceous perennials, little is known about the factors that govern it. The change to a flowering condition may be related to the accumulation of a certain amount of stored reserves (Harper and Ogden, 1970). Studies of many herbaceous perennials have demonstrated a correlation between plant size and reproductive status or fecundity (Bierzychudek, 1982b; Young, 1984; Kawano, Ohara, and Utech, 1986; Lovett Doust, Lovett Doust, and Turi, 1986; Smith, Ronsheim, and Swartz, 1986), but very little is known about the effects of age or growth rate on these traits. This lack of information is unfortunate, as size- and age-based demographic analyses have differ-

ent potential effects on demographic projections (Caswell, 1989). The relationship of size and age to demographically important parameters such as reproduction onset, survivorship, and fecundity should be determined and incorporated into population models (Hubbell and Werner, 1979; Law, 1983; Young, 1985; Hughes and Connell, 1987).

Studies relating both age and size to demographic characteristics of polycarpic perennial herbs seem to be rare primarily because for most herbaceous perennials, plant age cannot be determined. The understory herb *Trillium grandiflorum* is an exception as its age can be estimated (Brandt, 1916; Davis, 1981). In this paper we examine the relationship between age, leaf size, storage-organ size, and reproduction in *Trillium grandiflorum*. We use these data to determine the relative importance both of size and age in predicting reproductive status and of size in predicting age.

MATERIALS AND METHODS

Trillium grandiflorum (Michx.) Salisb. is a polycarpic perennial that occurs in the understory of deciduous woodlands throughout the Great Lakes region of North America and south through the Appalachian Mountains into North Carolina. The mature plant consists of a single stem (very rarely two), 15–45 cm high, arising from a short, tuberlike rhizome that bears long contractile roots. The stem bears a whorl of three leaves and a single terminal flower. *Trillium grandiflorum* does not reproduce clonally. *Trillium* rhizomes bear annual constrictions, which allow plant age to be estimated (Brandt, 1916; Davis, 1981). Estimated age will be most accurate for younger plants and will likely be a conservative estimate for older individuals since older portions of the rhizome can be lost through decay or physical damage.

Trillium grandiflorum seeds are dispersed by ants (Gates, 1940). The seeds germinate in the spring. The seedling develops primary and adventitious roots during the first growing season, but the cotyledon does not expand and become photosynthetic until the second growing season

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TABLE 1. Age, rhizome volume, and leaf area of reproductive and nonreproductive plants

	Reproductive		Nonreproductive		F
	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	N	
Annual constrictions	22.8 \pm 3.0	30	13.3 \pm 4.2	172	135.16****
Rhizome volume (cm ³)	5.48 \pm 2.29	30	1.10 \pm 1.05	172	287.39****
Total leaf area (cm ²)	53.00 \pm 12.77	29	17.50 \pm 12.88	129	180.56****

**** $P < 0.0001$.

(Patrick, 1973; Kalisz and Hanzawa, unpublished data). In the third season, *T. grandiflorum* produces one leaf. The transition from this one-leaf form to the three-leaved form evidently occurs when plants reach some minimum size (Kawano, Ohara, and Utech, 1986). In our field studies, both the large nonreproductive plants and all reproductive plants bear three leaves. The aboveground parts senesce by late summer. *Trillium grandiflorum* buds containing leaves and reproductive structures are well developed by the fall preceding their growing season (Hanzawa and Kalisz, personal observation).

The study was conducted in Long Woods, a 9.5-hectare oak-hickory forest that is part of the Kellogg Biological Station in Kalamazoo County, Michigan. *Trillium grandiflorum* occurs in patches throughout the understory of Long Woods. The study population covered an area of approximately 10 \times 15 m. In July 1989 all fruiting plants ($N = 57$) in this population were identified and marked. Fruits were bagged with netting just before dehiscence in mid- to late July. Seeds from all reproductive plants were collected and counted.

In early August we excavated all plants within a 10 \times 0.5-m transect through the population and excavated all reproductive plants within 3 m of this transect. The plants were transported to the lab. There we measured rhizome volume, leaf area, and age of each plant as follows. The rhizome of each plant was washed, and the stem was removed. Since we were unable to excavate entire root systems in all cases, the contractile roots and the leaves were removed before rhizome volume was measured. Next year's bud was left intact. The volume of rhizomes was

determined by measuring their displacement of water in the smallest graduated cylinder possible, which ranged from 10 ml to 50 ml. A Li-Cor LI-3100 Area Meter was used to measure leaf area to the nearest 1 mm². Since we were interested in the size of leaves produced by each plant, holes caused by herbivores were covered with tape before leaf area was measured. Plants were aged by counting the number of constrictions on the rhizomes. After data collection we replanted all rhizomes at their original sites.

To determine whether *T. grandiflorum* has a seed bank and to census for 1-year-old seedlings, in mid-August we removed soil to a depth of 10 cm from an 80 \times 80-cm quadrat adjacent to the sampling transect. A series of standard soil sieves was used to search this soil for *T. grandiflorum* seeds, first year seedlings (seedlings without expanded cotyledons), second year seedlings, and rhizomes. All *T. grandiflorum* rhizomes found in this quadrat were processed as described previously. The aboveground parts of many of these rhizomes had senesced before sampling or had not been produced that season. Therefore, for these rhizomes we have data on rhizome volume, age, and reproductive condition, but none on leaf area.

To determine correlations between size traits, age, and fecundity, Spearman correlations were calculated between age, rhizome volume, total leaf area, and fecundity for the entire sample and for reproductive and for nonreproductive plants separately. To quantify the relationship between rhizome volume and leaf area, we log-transformed the data and ran separate regressions of log(rhizome volume) on log(leaf area) for both reproductive

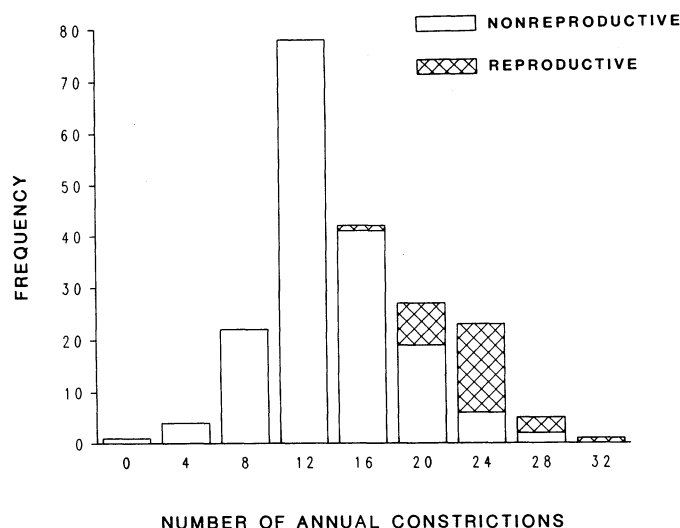


Fig. 1. Frequency distribution of number of annual constrictions of both nonreproductive and reproductive plants.

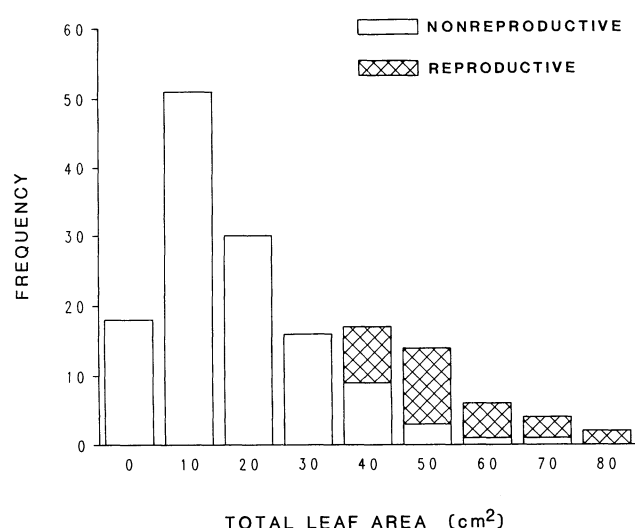


Fig. 2. Frequency distribution of total leaf areas of both nonreproductive and reproductive plants.

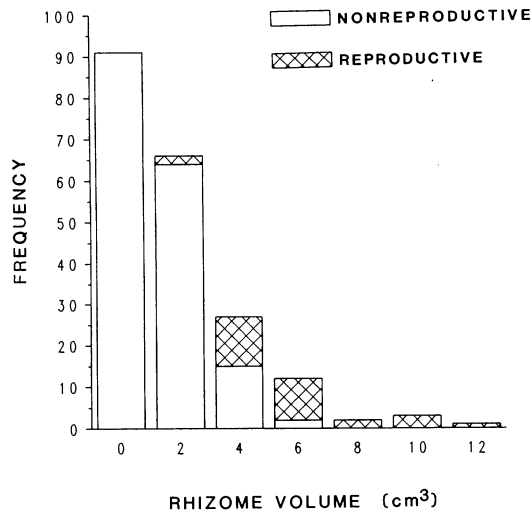


Fig. 3. Frequency distribution of rhizome volumes of both nonreproductive and reproductive plants.

plants and nonreproductive plants. To quantify the relationship between age and size measures, and seed set, we regressed fecundity on age, fecundity on leaf area, and fecundity on rhizome volume. All analyses utilized SAS statistical programs (SAS, 1985).

RESULTS

In our study population of *Trillium grandiflorum*, ages ranged from 1 to 30 years. The mean ages of nonreproductive plants (13.3 years) and of reproductive plants (22.8 years) differed significantly (Table 1). There was no seed bank. We found one 1-year-old seedling. Among sampled plants the range in total leaf area was 1.31–84.02

TABLE 2. Correlation coefficients (Spearman's *r*) between age, rhizome volume, total leaf area, and fecundity for: A. all plants sampled; B. reproductive plants; and C. nonreproductive plants. Sample sizes are in parentheses

	Age	Rhizome volume	Leaf area
A. All plants			
Rhizome volume	0.8670**** (202)		
Leaf area	0.7631**** (158)	0.9021**** (158)	
Fecundity	0.5568**** (201)	0.5794**** (201)	0.6096**** (158)
B. Reproductive plants			
Rhizome volume	0.5037** (30)		
Leaf area	0.5733** (29)	0.6569**** (29)	
Fecundity	0.3286 (28)	0.1517 (28)	0.2773 (28)
C. Nonreproductive plants			
Rhizome volume	0.7997**** (172)		
Leaf area	0.6249**** (129)	0.8430**** (129)	

** *P* < 0.01; **** *P* < 0.0001.

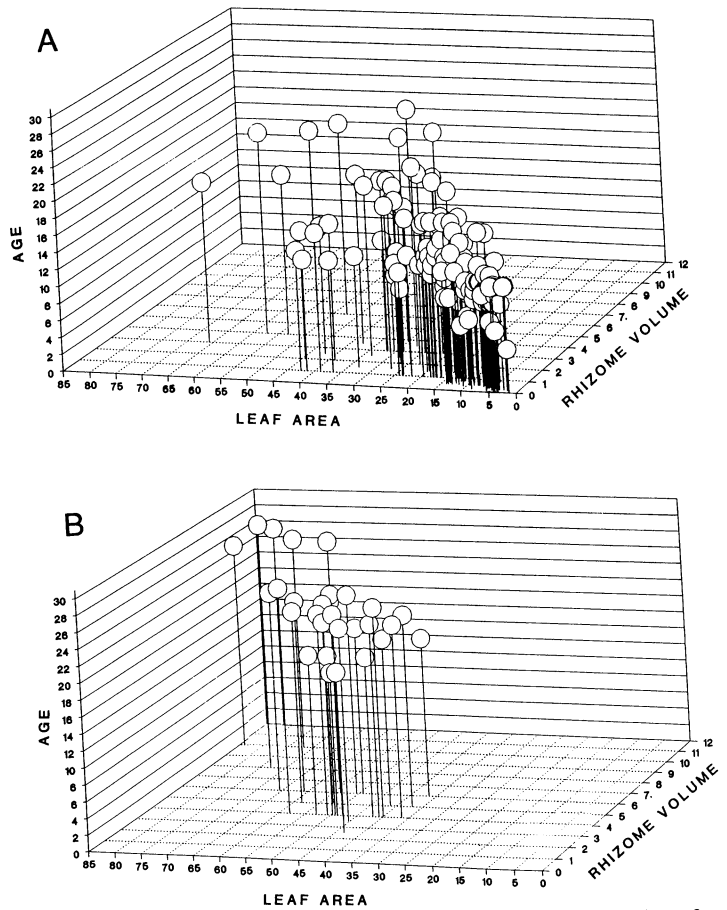


Fig. 4. Relationship between leaf area, rhizome volume, and age for (A) nonreproductive plants and (B) reproductive plants.

cm². The mean leaf areas of nonreproductive plants (17.50 cm²) and of reproductive plants (53.00 cm²) differed significantly (Table 1). Rhizome volumes ranged from 0.02 to 12.0 cm³. The mean rhizome volume of reproductive plants (5.48 cm³) was significantly greater than the mean rhizome volume of nonreproductive plants (1.10 cm³). Figures 1, 2, and 3 show, respectively, age, leaf area, and rhizome volume of reproductive and of nonreproductive plants.

Age, rhizome volume, total leaf area, and fecundity were highly correlated in the sampled population (Table 2A). Among reproductive plants, age, rhizome volume, and leaf area were correlated. Fecundity, however, was not significantly correlated with age, rhizome volume, or leaf area among reproductive plants (Table 2B). Age, rhizome volume, and total leaf area were correlated among nonreproductive plants (Table 2C).

The relationship between leaf area, rhizome volume, and age is shown in Figs. 4A (nonreproductive plants) and 4B (reproductive plants). All reproductive plants had total leaf areas greater than 36 cm² and were at least 17 years old. All reproductive plants had rhizome volumes greater than 2.5 cm³.

The relationship between log(leaf area) and log(rhizome volume) for both reproductive and nonreproductive plants is shown in Fig. 5. The slopes of the regression lines for the two classes did not differ significantly. For plants with

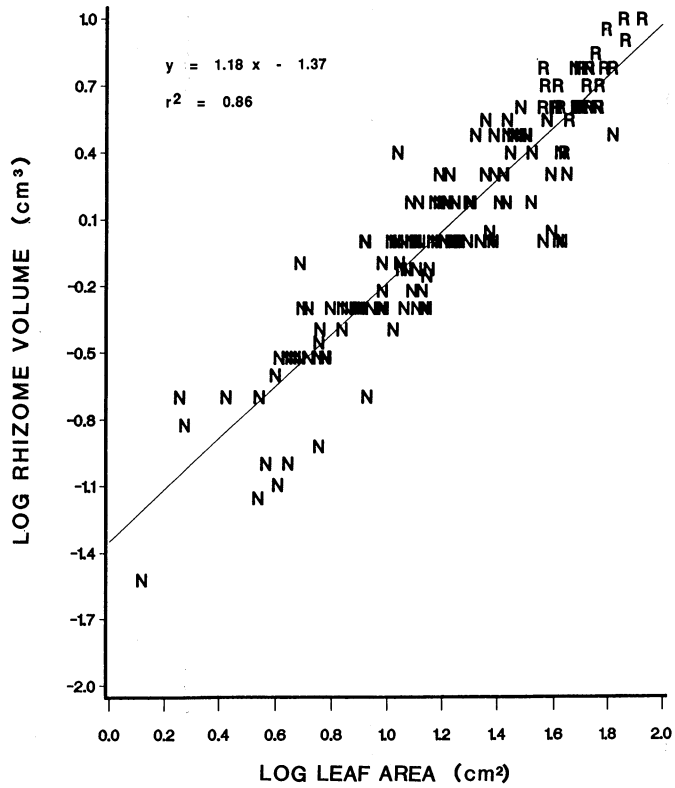


Fig. 5. Relationship between log(total leaf area) and log(rhizome volume) for nonreproductive (N) and reproductive (R) plants. For nonreproductive plants, $y = 1.08x - 1.28$. For reproductive plants, $y = 1.50x - 1.26$.

nonzero fecundity, the regressions of fecundity on age ($F = 1.64$; $df = 1, 26$; $P = 0.21$), fecundity on leaf area ($F = 0.97$; $df = 1, 25$; $P = 0.33$), and fecundity on rhizome volume ($F = 0.59$; $df = 1, 26$; $P = 0.47$; Fig. 6) were not significant.

DISCUSSION

Reproductive and nonreproductive *Trillium grandiflorum* plants differed significantly in both age and size. The ages of *Trillium grandiflorum* plants sampled ranged from 1 to 30 years. The reproductive plants had a minimum age of 17 and a mean age of 22.8 years, and were significantly older than the nonreproductive plants, which had a mean age of 13.3 years. These mean ages are similar to those of *T. erectum* (Davis, 1981). Reproductive and nonreproductive *T. erectum* had means of 20.6 and 14.5 constrictions, respectively. The long life span of *Trillium* is evidently typical of forest herbs (Bierzychudek, 1982a). In *Trillium* the number of constrictions on the rhizomes of older individuals may be considered conservative estimates of actual ages since the oldest portions of rhizomes may decay in the soil (Brandt, 1916; Davis, 1981). In addition to being older, on average, than nonreproductive individuals, reproductive individuals have significantly larger rhizome volumes and larger total leaf areas (Table 1).

The positive correlations of age, rhizome volume, and leaf area with fecundity in the sampled population (Table 2A) reflect the fact that a minimum size and/or age must

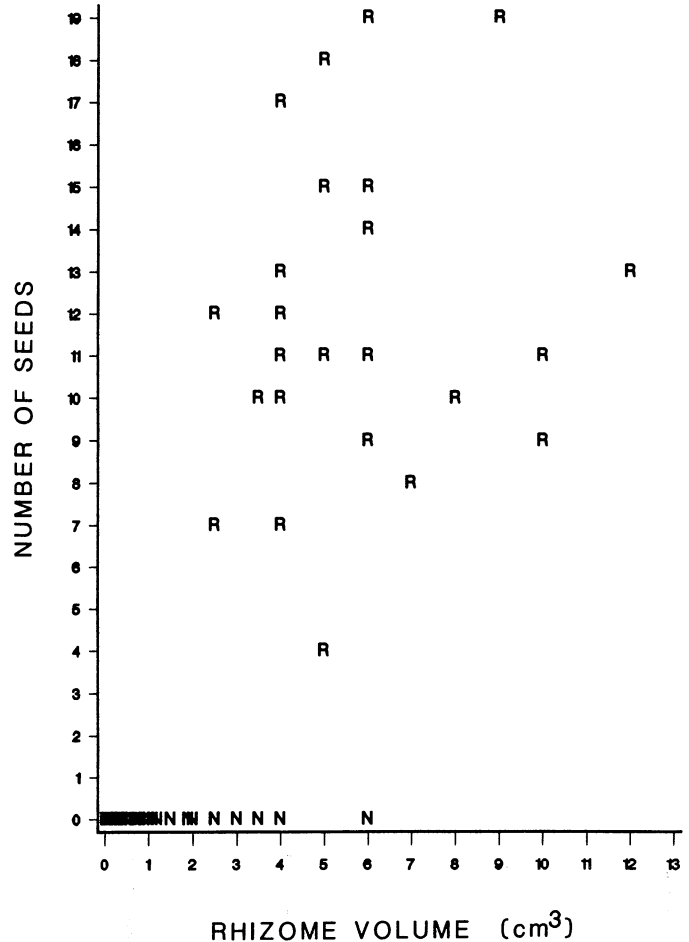


Fig. 6. Relationship between seed set and rhizome volume for reproductive (R) plants. The rhizome volumes of nonreproductive plants are shown for comparison (N).

be attained for any flowering to occur (Fig. 4). The positive correlation is due to the many plants smaller or younger than the minimum threshold, all of which had a fecundity of zero (Fig. 6). However, among *T. grandiflorum* plants that reproduced, rhizome volume did not have a significant relationship with fecundity (Table 2B). Age and leaf area were also uncorrelated with fecundity. Factors other than those measured in this study may determine seed set in this population. There are two potential explanations for the lack of correlation between rhizome volume, an estimate of stored resources, and realized fecundity. First, the amount of stored resources may determine flowering ability or probability, but other physiological or developmental traits may determine ovule production. Alternatively, the lack of correlation between seed set and plant resources may be explained by insufficient pollination and/or insufficient resource flow to developing ovules or seeds. Lubbers and Lechowicz (1989) found that seed set in *Trillium grandiflorum* may be pollinator limited in some, but not in all, years. Our study population flowered during a relatively cool, wet spring, which may have depressed pollinator number or activity. Our results seem to differ from those of Kawano, Ohara, and Utech (1986) who found a significant relationship between *T.*

grandiflorum seed set and total biomass. We plan to hand-pollinate plants in our population in order to document whether size and fecundity are correlated when supplemental pollen is available.

When polycarpic plants become reproductive, resources must be allocated to the production of reproductive as well as vegetative structures. Because resources are finite, trade-offs are presumed to occur between allocations to growth, reproduction, and storage (Law, 1979; Reekie and Bazzaz, 1987a, b, c). Thus, if such trade-offs occurred and rhizome volume estimated the amount of resources, the relationship between rhizome volume at the time of allocation and leaf area during the subsequent growing season would be expected to differ in reproductive and nonreproductive plants. By this model, it would be expected that the increment in leaf area for a given increment in rhizome volume would be less for reproductive than for nonreproductive plants inasmuch as a portion of the stored resources in the former is being allocated to reproduction in addition to storage and growth. However, our data show no significant difference between plants in these groups in the relationship between $\log(\text{leaf area})$ and $\log(\text{rhizome volume})$. Since *T. grandiflorum* forms buds containing leaves and reproductive structures during the fall preceding a growing season, ideally, the rhizome volume should be measured at that time. However, the measurement of rhizome volume required the removal of all roots. As this removal had the potential to affect subsequent allocation patterns, we measured rhizome volume and leaf area at the same time.

Our data show that size is a better predictor of reproductive status than is age. There seems to be a minimum size below which plants do not reproduce, regardless of age. We found no reproductive plants with leaf areas smaller than the threshold value of 36.27 cm² or rhizome volumes smaller than the threshold value of 2.50 cm³ (Fig. 4). Of plants with leaf areas equal to or greater than the threshold value, 70% reproduced. Of plants with rhizome volumes equal to or greater than the threshold value, 58% reproduced. In contrast, of plants at or above the age threshold for reproduction (17 years), only 45% reproduced. Thus, both leaf area and rhizome volume were better predictors of plant reproductive status than was age. In *Podophyllum peltatum*, a rhizomatous polycarpic herb that co-occurs with *T. grandiflorum* at our study site, rhizome size (as measured by the length of the ultimate rhizome internode) was the best predictor of flowering of a shoot (Sohn and Policansky, 1977). Among nonannual plants, size is generally a better predictor of the onset of flowering than is age (Lacey, 1986). However, Young (1985) points out that the existence of an evident size threshold for reproduction does not mean that other factors such as age or growth rate do not also affect the onset of reproduction or other demographic parameters such as survivorship or fecundity.

Although most *T. grandiflorum* individuals above the size threshold reproduced, a significant fraction did not. Plants making a large investment in reproduction in one year may have a lower probability of flowering in the subsequent year or years because stored resources are depleted by the large reproductive effort. This pattern has been observed in other herbaceous perennials. For example, successful fruit set in one season decreased the

probability of future flowering in both *Podophyllum peltatum* (Sohn and Policansky, 1977) and *Tipularia discolor* (Snow and Whigham, 1989). Minimal production and storage of photosynthate within a season may similarly result in decreased probability of emergence in the subsequent season and, among the emergent plants, in decreased probability of flowering. Such a phenomenon would explain both the sizable fraction of *T. grandiflorum* rhizomes without aboveground parts found in soil samples and also the frequent occurrence of large nonreproductive individuals. Similar results have been observed in experimentally defoliated *Jeffersonia diphylla*, an understory herb that resembles *Trillium* in having a perennating rhizome but no permanent aboveground parts (Smith, Ronsheim, and Swartz, 1986). The same study found that some reproductive plants that were totally defoliated did not emerge the following year. Those emerging did not flower and had fewer and smaller leaves than in the preceding year. Interestingly, 50% defoliation of flowering *J. diphylla* had no effect on reproductive status or seed set in either the season in which plants were defoliated or the season following.

Similarly, the effects of partial defoliation and/or large reproductive effort on current or subsequent growth or on fecundity of *T. grandiflorum* may be observed only when these factors result in a particularly great drain on stored resources. Lubbers and Lechowicz (1989) looked for trade-offs within one season between seed set and accumulation of resources in the rhizome of flowering *T. grandiflorum*. A consistent negative correlation between seed set and current year's storage existed only at high levels of experimental defoliation (50% or 75% of leaf area removed). Partial defoliation or increased current reproduction resulting in no decrement in storage may not affect subsequent growth or fecundity. We are collecting, as part of a long-term study, yearly data on leaf area, flower production, fruit production, and fecundity. These data will allow us to document the effects of growth rate, reproduction, and herbivory within a season on subsequent emergence, reproductive status, and fecundity. We will also be able to identify whether there is a specific size at which the transition from nonreproductive to reproductive status occurs. As plant age, size, and growth rate can all be estimated, *T. grandiflorum* is a model system in which studies of demography, ecology, and genetics can be integrated.

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