

# The effect of experimental defoliation on the growth and reproduction of a woodland orchid, *Tipularia discolor*

DENNIS F. WHIGHAM

Smithsonian Environmental Research Center, Edgewater, MD 21037, U.S.A.

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Leaves of individuals of *Tipularia discolor* were subjected to 3 years of manual defoliation to simulate natural patterns of herbivory. Compared with controls, plants that were 100% defoliated did not reproduce sexually after two defoliations, the biomass of new belowground corms decreased significantly in the 1st year and each year thereafter, and leaf biomass declined significantly after three defoliations. Senescence of belowground corms and mortality of entire plants were highest in the 100% defoliation treatment. The responses of plants with 50% defoliation were intermediate. The study demonstrates that belowground corms are the first biomass component to be negatively impacted by complete and partial defoliation. Reductions in corm biomass resulting from leaf herbivory would eventually reduce leaf biomass and sexual reproduction.

**Key words:** woodland herb, herbivory, biomass allocation, reproduction, *Tipularia discolor*, Orchidaceae, defoliation.

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Des individus de *Tipularia discolor* ont été défoliés manuellement pendant 3 ans en simulant le patron naturel de broutage. Comparés aux témoins, les plants défoliés à 100% ne se sont pas reproduits sexuellement après deux défoliations, la biomasse de leurs cormes souterrains nouvellement formés a diminué de façon significative au cours de la 1<sup>re</sup> année et de chaque année subséquente et, après trois défoliations, leur biomasse foliaire a diminué de manière significative. C'est dans ce même groupe qu'on a également noté la sénescence des cormes souterrains et la mortalité des plants entiers la plus élevée. La réaction des plants défoliés à 50% a été intermédiaire. L'étude a démontré que ce sont les cormes souterrains qui représentent la première composante de la biomasse à être affectée négativement par la défoliation qu'elle soit partielle ou complète. La réduction de la biomasse des cormes résultant du broutage par les herbivores pourrait éventuellement réduire la biomasse foliaire et la reproduction sexuée.

**Mots clés :** herbe forestière, broutage, allocation de biomasse, reproduction, *Tipularia discolor*, Orchidaceae, défoliation.  
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## Introduction

Herbivory can enhance, diminish, or have little impact on plant performance (Belsky 1986; Crawley 1983; Meagher and Thompson 1987). In some graminoids, herbivory stimulates the production of leaf biomass (Coughenour et al. 1985a; McNaughton 1986), whereas in other plants it has a negative effect (Coughenour et al. 1985b; Danell et al. 1988; Kinsman and Platt 1984). Woody species often produce additional leaf biomass following defoliation (Bergstrom and Danell 1987; Crawley 1983; Mendoza et al. 1987), but chronic herbivory almost always has negative effects on plant performance (Crawley 1983).

There have been few studies of the impact of herbivory on long-lived forest herbs (Bratton 1974; Cook 1979, 1985; Falinski 1986; Inghe and Tamm 1987; Lubbers and Lechowicz 1989; Maekawa 1926; Newell et al. 1981; Pitelka et al. 1985; Schaffner 1922; Smith et al. 1986; Solbrig et al. 1988) and even fewer studies in which the responses to defoliation of aboveground and belowground plant parts have been measured simultaneously (Lubbers and Lechowicz 1989). Leaf herbivory may be infrequent in some species of woodland herbs (Inghe and Tamm 1985, 1987; Kawano 1985; Kawano et al. 1982; Pitelka and Ashmun 1985; Pitelka et al. 1985; Solbrig et al. 1988) but frequent in others (Whigham and O'Neill 1988). In this paper I report the results of a 3-year study of experimental defoliation of *Tipularia discolor*. The objective of the study was to quantify the temporal effects of annual experimental defoliation on the growth of leaves and belowground corms, on senescence of corms, and on sexual reproduction.

## Species and site descriptions

Aspects of the ecological life history of *T. discolor*, a common orchid in the deciduous forests of eastern North America, have been described by Whigham (1984). It is a long-lived winter green perennial (Givnish 1986) that usually produces only one leaf and one belowground corm per year. Because corms usually live for more than 1 year, individuals normally have three or four corms, but the number is variable (Efird 1987; Whigham 1984; Snow and Whigham 1989). Vegetative propagation occurs when a plant initiates two corms rather than one, and it is most common on plants that have flowered (Efird 1987; Snow and Whigham 1989). Flowering occurs in August while the plants are leafless (Whigham and McWethy 1980). Leaves, which appear in September and senesce in May–June, develop on corms produced in the previous year (Whigham 1984). White-tailed deer (*Odocoileus virginianus*) are the primary herbivores of *Tipularia* leaves, and they almost always completely remove the entire leaf. Leaf herbivory can be high in *Tipularia*, and most plants do not go more than 2–3 years without having their leaves eaten (Whigham and O'Neill 1988).

Two characteristics make *Tipularia* an ideal test species for an experimental defoliation study. (i) Most plants are shallow rooted, and the sizes of individual corms can be measured "in-the-ground." This makes it possible to quantify the effect of experimental defoliation on net annual corm biomass production and on corm senescence. (ii) There is a close relationship between corm biomass and leaf size (area and biomass) (Efird 1987; Snow and Whigham 1989). The biomass of a corm pro-



duced in a growing season is positively related to the area and biomass of the leaf that was produced at the beginning of the growing season, which in turn is positively related to the biomass of the corm that was produced during the previous growing season. The close relationship between leaf biomass and corm biomass makes it possible to quantify the temporal influence that experimental defoliation has on the relationships between corm biomass and future growth and reproduction.

The study was conducted in an upland hardwood forest on the property of the Smithsonian Environmental Research Center near Annapolis, Maryland. Details of the site can be found in Whigham and McWethy (1980) and Whigham (1984).

### Methods

During the 2nd week of October 1984, 75 plants were randomly chosen within an area used for previous studies (Whigham and McWethy 1980; Whigham 1984; Snow and Whigham 1989). Each plant was randomly assigned to one of two treatment groups or to the control group (25 individuals per group). The length (L) and width (W) of each leaf was measured to the nearest 0.1 cm. The number of corms on each plant was counted, and the length (CL) and width (CW) of each corm was measured to the nearest 0.1 mm with an electronic caliper. Leaf and corm biomass at the beginning of the study did not differ among the three groups. After the initial measurements were made, leaves were completely removed from one treatment group by severing the petiole. The other treatment group had the top half of each leaf removed.

Initial responses to defoliation were determined in May 1985 when the lengths and widths of new corms produced during the growing season (October–May) were measured. The number of older corms was counted for each plant. Plants were again censused in early August during anthesis, and the number of flowers per inflorescence counted. Two weeks later, the number of fruits per inflorescence was counted. Fruit counts were repeated monthly between September and November to determine if any fruit abortion had occurred. Leaf manipulations, measurements of leaves and corms, and counts of flowers, fruits, and the number of corms per plant were repeated in 1985, 1986, and 1987.

Leaf and corm length and width data were converted to estimates of leaf biomass (LW) and corm biomass (CB), measured in grams, using regression equations developed in preliminary studies ( $LW = 0.0099 + 0.0031 (L \times W)$ , where  $r^2 = 0.96$ ,  $N = 42$ ,  $P < 0.0001$ ; and  $CB = 0.00224 (CL \times CW)$ , where  $r^2 = 0.91$ ,  $N = 42$ ,  $P < 0.001$ ). Repeated measures analysis of variance was used to test for treatment, year, and year  $\times$  treatment interactions for leaf and corm biomass and the number of corms per plant. The significance of treatment was tested against the plant nested in treatment error term. Two-way analysis of variance was used to test for treatment, year, and treatment  $\times$  year effects on the number of flowers per inflorescence and percentage of flowers that became fruits (Joyner 1985). Percent data were arcsine and square root transformed before analyses. Means were compared using the Tukey honestly significant difference test and least squares means comparisons. Plants that experienced natural herbivory in the control and 50% defoliation groups were excluded from the analyses.

### Results

There were significant treatment ( $P \leq 0.0001$ ) and year  $\times$  treatment ( $P \leq 0.013$ ) effects on leaf biomass (Fig. 1). Plants that were 100% defoliated had significantly smaller leaves than did plants in the other two groups. The significant interaction effect was due to smaller leaves on plants in the 100% defoliation group in 1986 and 1987 (Fig. 1). The year effect was not significant for the 50% defoliation and control groups.

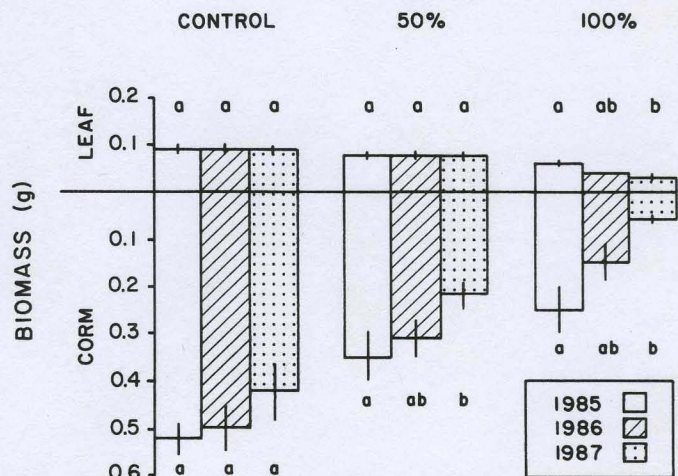


FIG. 1. Estimated leaf and new corm biomass (g) of plants in the control and two treatment groups (50 and 100% defoliation). The linear regressions used to estimate leaf and corm biomass are given in the Methods section. Leaf and corm biomass prior to the first defoliation were similar for each group. Defoliation was initiated in 1984 and continued for 3 years (1985, 1986, and 1987). Values are means  $\pm 1$  SE. Means that are not different within treatments share the same letters.

TABLE 1. Number of corms ( $\pm 1$  SE) per plant for the control and 50 and 100% defoliation groups at the beginning of the experiment (1984) and after 3 years

	Control	50%	100%
1984	3.6 $\pm$ 0.4a	3.5 $\pm$ 0.2a	3.8 $\pm$ 0.2a
1985	3.6 $\pm$ 0.3a	3.3 $\pm$ 0.2a	3.2 $\pm$ 0.4a
1986	3.3 $\pm$ 0.3a	2.9 $\pm$ 0.2ab	2.6 $\pm$ 0.5ab
1987	3.3 $\pm$ 0.3a	2.6 $\pm$ 0.2a	2.3 $\pm$ 0.3b

NOTE: Within-treatment means that are not significantly different are followed by the same letter.

There were significant year ( $P \leq 0.001$ ) and treatment ( $P \leq 0.0001$ ) effects on the biomass of new corms. The interaction effect was not significant. The mean biomass of new corms of all three groups was significantly different from each other ( $P \leq 0.05$ ). Biomass of new corms in the two defoliation groups decreased significantly after one defoliation (Fig. 1). By the end of the third growing season, the mean biomass of new corms in the 50% defoliation group ( $0.23 \pm 0.02$  g) was 48% less than that in the control group ( $0.44 \pm 0.05$  g). The mean biomass of new corms in the 100% defoliation group ( $0.07 \pm 0.01$  g) was only 16% as large as that in the control group by the 3rd year. No plants died in the control and 50% defoliation groups during the 3 years of the study, whereas one plant in the 100% defoliation group died during the 2nd year and five during the 3rd year.

There was no significant difference between the three groups in the number of corms per plant at the beginning of the study (Table 1). By the 3rd year, the number of corms per plant decreased significantly ( $P \leq 0.05$ ) in the two defoliation groups. Because all plants produced at least one new corm per year, the decrease in the number of corms per plant in the two defoliation groups could have been due only to a faster rate of senescence of older corms.

The number of plants that flowered differed significantly (test of independence:  $G = 93.606$ ,  $df = 2$ ,  $P < 0.001$ ).



TABLE 2. Comparison of the number of flowers ( $\pm 1$  SE), percentage of flowers that developed into fruits ( $\pm 1$  SE), and percentage of plants in each treatment group that flowered during the 3 years of the study

	1985	1986	1987
Control			
% flowering	48 (8)	25 (6)	29 (6)
No. of flowers	29.6 $\pm$ 1.7a	34.5 $\pm$ 1.8a	29.8 $\pm$ 2.5a
% fruit set	32.8 $\pm$ 7.2a	17.3 $\pm$ 7.0a	15.7 $\pm$ 6.1a
50% defoliation			
% flowering	42 (8)	33 (7)	10 (2)
No. of flowers	29.1 $\pm$ 0.9a	34.0 $\pm$ 2.9a	30.5 $\pm$ 2.5a
% fruit set	34.5 $\pm$ 10.4a	13.9 $\pm$ 3.2a	1.5 $\pm$ 1.5a
100% defoliation			
% flowering	65 (11)		
No. of flowers	32.8 $\pm$ 1.4	None	None
% fruit set	43.9 $\pm$ 3.5		

NOTE: Means within the same row that are followed by the same letter are not significantly different. Sample sizes are given in parentheses. Data for the 100% defoliation group were not included in the ANOVA because plants did not flower in 2 years, and the data, therefore, were not normally distributed.

Between 42 and 65% of all plants flowered the first summer after the defoliation experiment began (Table 2). No plants flowered after that year in the 100% defoliation group. The percentage of plants that flowered during the 2nd year in the 50% defoliation group (33%) was greater than the percentage of plants that flowered in the control group (25%). By the 3rd year, the percentage of plants that flowered decreased to 10% (two plants) in the 50% defoliation group compared with 29% (six plants) in the control group.

Leaf manipulation had no effect on the number of flowers per inflorescence (Table 2). Leaf manipulation also had no significant effect on fruit set, even though the data show large between-year differences and a striking decrease in fruit set for the 50% defoliation group in 1987. There was no fruit abortion for any group during 3 years of the study.

### Discussion

Herbivory should have an impact on the growth and reproduction of perennial woodland herbs because most species maintain a large percentage of their total biomass in belowground structures (Abrahamson 1979), and the stored energy and nutrients are used to support growth and reproduction (Kawano 1985; Pitelka et al. 1985; Snow and Whigham 1989; Whigham 1984). Results of several recent long-term studies of populations of woodland herbs indicate that some form of herbivory was common and that it probably had a negative effect on future growth and reproduction (Falinska 1985; Inghe and Tamm 1985, 1987; Kawano 1985; Solbrig et al. 1988). None of the authors, however, had detailed observational data to support their statements, nor did they document the degree to which belowground biomass was used to support future growth and reproduction in response to herbivory. In single defoliation studies, Smith et al. (1986) found that partial or complete defoliation had little impact on reproduction of *Jeffersonia diphylla*. They speculated that *Jeffersonia* responded to partial defoliation by increasing photosynthetic rates. Completely defoliated plants compensated by producing new leaves. In *Thalictrum thalictroides*, Lubbers (1982) found that removal of the upper cauline leaves reduced seed production but had no effect on belowground storage. In

contrast, Lubbers and Lechowicz (1989) found that defoliation of *Trillium grandiflorum* resulted in a decrease in belowground storage but had little effect on sexual reproduction. In this longer term study, I have demonstrated that removal of 50 and 100% of the leaf biomass resulted in a significant decrease in both future growth (leaf weight and corm biomass) and sexual reproduction. The study also demonstrates that not all plant characteristics are equally affected by defoliation. The number of flowers per inflorescence and fruit abortion responded least to defoliation. Leaf biomass was more conservative than corm biomass and whether or not a plant flowers.

*Tipularia*, like other woodland herbs (e.g., Menges 1987), clearly utilized corm biomass, most likely total nonstructural carbohydrates (Lubbers and Lechowicz 1989), to compensate for the loss of leaf tissue. Maekawa (1926) and Schaffner (1922) showed that *Arisaema* spp. switch from female to male plants or from male to asexual plants following a single defoliation. The changes in *Arisaema* were also most likely due to a decrease in the biomass of the corms. The high energy and nutrient costs associated with sexual reproduction (Silva 1978; Snow and Whigham 1989; Sohn and Policansky 1977) would explain why flowering ceased in the 100% defoliation group. Defoliation also reduced the amount of flowering in *Epidendrum radicans* (Yoneda and Sasaki 1978). Sexual reproduction was also the most sensitive life-history stage of another long-lived woodland herb (*Uvularia perfoliata*) that I studied in a similar type of forest (Whigham 1974).

Corm biomass in the 50% defoliation group declined at a lower rate, and it took three defoliations before the frequency of flowering decreased. Plants in the 50% defoliation group also set fewer fruits after three defoliations. In contrast with Lubbers and Lechowicz (1989), results from this study show that intermediate levels of herbivory can have a negative effect on sexual reproduction, even though plants may still be able to flower. The fact that there was no decrease in the number of flowers per inflorescence for any flowering individuals indicates genetic, rather than resource, control of flower number.

These results also suggest that defoliation could partially explain the decrease in mean leaf area of individuals in populations of *Tipularia* that we have been monitoring for more than 10 years (Whigham and O'Neill 1988). All of our marked plants have experienced at least one complete defoliation during the study, and most have been defoliated several times and, quite often, for 2 or more years in succession. Because of the close relationship between new corm biomass and leaf size (Efrid 1987; Snow and Whigham 1989), a single 100% defoliation would result in a significant decrease in corm biomass. There would not be a significant decrease in leaf biomass after one defoliation because resources stored in older corms could be used to support future leaf growth. Two or more years of successive defoliation could, however, result in a significant decrease in leaf biomass as the amount of resources in corms continued to decline.

This study clearly shows that defoliation can have a large impact on the future growth and reproduction of *Tipularia* and lends support to the findings of Lubbers and Lechowicz (1989) that immediate reproductive gains may be more important than future fitness as measured by the size and number of belowground storage structures. These findings are most likely representative of nonclonal species or clonal species whose ramets are physiologically independent (Ashmun et al. 1982; Flanagan and Moser 1985) and least likely representative of clonal woodland herbs with ramets that are physiologically



integrated (e.g., Hutchings and Bradbury 1986; Sohn and Policansky 1977).

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