

## How experimental defoliation and leaf height affect growth and reproduction in *Trillium grandiflorum*<sup>1</sup>

Thomas P. Rooney and Donald M. Waller

Department of Botany, University of Wisconsin-Madison, 430 Lincoln Drive, Madison WI 53706

ROONEY, THOMAS P. AND DONALD M. WALLER (Department of Botany, University of Wisconsin-Madison, 430 Lincoln Drive, Madison WI 53706). How experimental defoliation and leaf height affect growth and reproduction in *Trillium grandiflorum*. *J. Torrey Bot. Soc.* 128: 393–399. 2001.—Both defoliation and higher leaf placement can reduce growth in herbaceous plants. We examined variation in relative growth rate (RGR) and reproduction in response to defoliation and leaf height in *Trillium grandiflorum* at 4 sites in northern Wisconsin, USA. Plant biomass and the probability of flowering increased with increased leaf height. Analyses of covariance revealed that experimental defoliation and leaf height separately and independently reduced individual RGR, and accounted for about 42% of the total variance in RGR. Defoliation in 1998 had no effect on flowering in 1999, but leaf height in 1998 was positively associated with the likelihood of flowering in 1999. RGR and plant responses to defoliation varied among sites. We conclude that defoliation and leaf height reduce RGR over short time scales.

Key words: perennial forest herb, herbivory, cost of height, undercompensatory growth.

Just as a business earns a profit when revenues exceed its operating costs, a plant experiences a net carbon gain when net carbon assimilation exceeds the construction and maintenance costs of its roots and shoots (Blackman 1919; Evans 1972; Mooney and Gulmon 1982; Chapin et al. 1990). Net carbon assimilation can be studied using growth analysis: a technique that involves sequentially measuring plant size and deriving rates of change (Evans 1972; Hunt 1982). Reproduction in most perennials depends on size rather than age (Harper 1977; Caswell 1989). Although many factors affect plant growth rates and reproduction, our research focuses on two seemingly disparate factors: defoliation and leaf height. Both factors potentially reduce net carbon gain, but in different ways: defoliation reduces the photosynthetic capacity of plants and net carbon assimilation, while higher leaf placement increases shoot construction and maintenance costs. Here we report how defoliation and leaf height affect shoot growth rates and flowering in the perennial temperate forest herb, *Trillium grandiflorum*. (Michx.) Salisb. (Gleason and Cronquist 1991).

Like other temperate forest herbs, *T. grandiflorum* has a dormant phase and an active phase.

At the beginning of the active phase of the cycle, plants mobilize reserves from a below-ground rhizome to build the above-ground shoot, which consists of leaves needed for energy capture and stems to support those leaves (Chapin et al. 1990). All carbon assimilation occurs during this active phase. At the end of this phase, the shoot senesces, and the plant enters dormancy. In “good” years, carbon assimilation exceeds construction and maintenance costs, and the plant is able to build a larger shoot the following season. Plants have “bad” years when construction and maintenance costs exceed carbon assimilation. In response to bad years, plants may experience a net carbon loss, causing the shoot to shrink in stature in the following season (e.g., Bierzychudek 1982). *Trillium grandiflorum* plants can flower once they reach a minimum size (typically >15 cm tall), although surpassing a size threshold alone is not sufficient for reproduction (Hanzawa and Kalisz 1993).

The effects of defoliation depend in part on the timing of defoliation (Maschinski and Whitham 1989; Whitham et al. 1991; Doak 1992). Theory predicts that damage to plants is greatest shortly after new leaves and stems emerge, and least severe at shoot senescence. In the latter case, the plant is able to photosynthesize throughout the season, and thus potentially assimilate more carbon than was expended for the construction and maintenance of shoots. In the former case, shoot construction costs are seldom recovered. Several studies show that defoliating forest herbs in one season reduces their size and probability of reproducing during the next growing season (Table 1). Defoliation decreases net

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Table 1. Some perennial forest herbs that exhibit an undercompensatory response to 100% defoliation.

Species	Trait negatively affected	Author
<i>Sanguinaria canadensis</i>	reproduction only <sup>1</sup>	Rockwood and Lobstein (1990)
<i>Aralia nudicaulis</i>	plant size, reproduction	Edwards (1985)
<i>Clintonia borealis</i>	plant size, reproduction	Balگوoyen and Waller (1995)
<i>Tipularia discolor</i>	plant size, reproduction	Whigham (1990)
<i>Cypripedium acaule</i>	plant size, reproduction	Primack et al. (1994)
<i>Trillium grandiflorum</i>	plant size, reproduction	Anderson (1994) Augustine and Frelich (1998)
<i>Maianthemum canadense</i>	plant size, reproduction	Rooney (1997)
<i>Arisaema triphyllum</i>	plant size, reproduction	Ruhren and Handel (2000)

<sup>1</sup> Plant size was not examined in this study.

carbon assimilation and thus represents a cost. Leaf height, in contrast, involves a trade-off between photosynthetic rate per unit shoot mass and the structural cost of leaf height. Theory predicts that the proportion of shoot biomass allocated to leaves declines as absolute leaf height increases, because there is a disproportionate increase in the stem mass required to maintain mechanical stability (Givnish 1982; 1986a). Because leaf height increases as plants grow larger (Anderson 1994; Irwin 2000), construction and maintenance costs increase with leaf height. Thus, the decline in fractional allocation to photosynthetic organs relative to whole plant size and the absolute increase in plant biomass with increasing plant stature both represent a cost of leaf height. Although both defoliation and leaf height should affect plant growth, the relative importance of each for net carbon gain is unknown.

This study examines how leaf height and defoliation affect growth and reproduction in *T. grandiflorum*. We evaluated the costs of leaf height and defoliation in this plant by conducting a replicated field experiment in a forested landscape. We hypothesized experimental defoliation would reduce plant growth rates and the probability of flowering the following season. We also hypothesized plant growth rates would decline, and the probability of flowering would increase with increasing leaf height. This project was motivated in part by recent studies (Anderson 1994; Augustine and Frelich 1998) and our own observations that white-tailed deer (*Odocoileus virginianus*) can have substantial impacts on *T. grandiflorum* populations.

**Methods and Materials.** *Trillium grandiflorum* individuals are nonclonal and persist underground in a dormant state during autumn and winter. In northern Wisconsin, leaves appear aboveground approximately one week before

forest canopy leaf-out, often the first week of May. Individuals remain photosynthetically active until mid- to late-summer, when leaf senescence occurs (typically in August). At senescence foliar nutrients are reabsorbed, and the plant enters its dormant state until the following spring (Case and Case 1997). Several other forest herbaceous species, including plants in the genera *Podophyllum*, *Asarum*, *Arisaema*, *Smilacina*, *Polygonatum*, *Medeola*, *Uvularia*, *Streptopus*, and *Panax*, show a similar phenological pattern, and have been classified by Givnish (1982, 1987) as "early summer species" in his photosynthetic guild scheme. Members of this guild show several convergent traits; among these is convergence in growth form. Members of this guild hold their leaves in an arching or umbrella-like manner which minimizes self-shading and maximizes light interception beneath a closed forest canopy (Givnish 1982, 1987).

We conducted this study in Forest and Ashland Counties, in the northern mesic forest region of Wisconsin, USA (Curtis 1959). According to unpublished Wisconsin Department of Natural Resources (DNR) data, there were approximately 9.8 deer km<sup>-2</sup> at the Ashland Co. sites and 17.9 deer km<sup>-2</sup> at the Forest Co. sites. In both counties, deer densities exceeded population goals established by the DNR by a factor of 2 (Rooney 2000).

In 1998, we established a single 5 × 5 m plot at each of 4 sugar maple-dominated stands that contained *Trillium grandiflorum*. Plots were similar with respect to light and fertility (Rooney 2000). Inside each plot, we permanently marked 20 plants by placing a numbered tag 20 cm south of the plant (n = 80 plants). Approximately 1 week after flowers opened and the anthers dehisced, we measured the leaf height of each plant (from the ground to the leaf petioles) to the nearest 5 mm. We then randomly assigned

5 flowering and 5 non-flowering plants in each study plot to each of two treatments: defoliated and intact (as a control). Plants in the defoliation groups were clipped on May 16–17, 1998. All of the leaf biomass and the upper portion of the stem were removed to mimic deer browsing (Augustine and Frelich 1998). Plots were revisited in 1999, and marked plants were re-measured approximately 1 week after anther dehiscence.

Size-related morphological traits, such as leaf height and leaf area, are often correlated (Niklas 1994). Therefore, measurement of a single size-related trait should provide a reliable estimate of plant size (Anderson 1994). To test this hypothesis, we collected morphological data from 54 flowering plants. These plants were randomly selected from plants outside of our study plots. We included leaf height measured to the nearest mm (from the ground to the height of the leaf petiole), stem diameter measured to the nearest 0.01 mm (approximately 3–4 cm from the ground), leaf area to the nearest mm<sup>2</sup>, and sepal area measured to the nearest mm<sup>2</sup>. We performed a principal components analysis on all of these variables (except leaf height) arranged in a correlation matrix. We saved the factor scores for the first axis (PC1), and examined the relationship between this axis and leaf height using regression analysis. A significant result indicates that leaf height is a reliable estimate of plant size.

We used logistic regression to examine the effects of defoliation and height on reproduction, because the response variable reproduction is categorical (flowering or not flowering). We performed two statistical tests. In the first, we examined the relationship between the defoliation treatment and flowering in 1999. In the other, we used the natural log of leaf height in 1998 as the predictor variable, and flowering in 1999 as the response variable.

Reliable analysis of plant growth requires measuring plant biomass (Evans 1972; Chiarello et al. 1989). This is not possible in a study that employs repeated measures of the same individual. We therefore tracked plant growth using leaf height as a surrogate for aboveground dry weight biomass. To calibrate this relationship, we measured the leaf height and then collected the aboveground portion of 16 flowering individuals from outside our study plots. We dried stems, leaves, and flowers to constant weight (in mg) at 70°C. We examined the relationship between the proportional allocation to leaves (leaf

biomass/stem + leaf + flower biomass) and leaf height using regression analysis. Next we natural log transformed aboveground biomass and height, and used regression analysis to infer aboveground plant biomass from leaf height ( $n = 16$ ;  $r^2 = 0.68$ ;  $P < 0.001$ ;  $\ln \text{ biomass} = -3.83 + 1.86 \ln \text{ height}$ ). In *Trillium grandiflorum*, aboveground and belowground biomass are correlated (Kalisz and Hanzawa 1993). Therefore, measurements of leaf height should provide an approximate estimate of belowground biomass and total plant biomass. Next, we calculated relative growth rate (RGR) according to the equation:  $\text{RGR} = \ln(\text{est. biomass in 1999}) - \ln(\text{est. biomass in 1998})$  (Evans 1972). While we only measured aboveground RGR, we recognize that aboveground growth rates usually reflect whole-plant growth rates (Shipley 1989).

We analyzed how defoliation and leaf height in 1998 (covariate) affected RGR via a one-way analysis of covariance (ANCOVA). To examine the variation in RGR attributable to study site, we analyzed differences in RGR among our study sites using one-way ANOVA. We calculated the mean RGR ( $\pm 1$  SE) for each of the 4 study sites, and use a one-way ANOVA followed by Tukey's B procedure to test for significant differences in RGR among sites. Lastly, we examined the simultaneous roles of experimental defoliation and site on RGR using a two-way ANCOVA. Pre-defoliation leaf height in 1998 was again used as the covariate.

**Results.** White-tailed deer ate 21 of the 80 plants (26%) before they were re-measured in 1999, preventing us from analyzing data from these plants. Of the 59 remaining plants, 46% flowered in 1998. All plants that were defoliated in 1998 ( $n = 31$ ) failed to send up a new shoot later in the same growing season. However, all control plants ( $n = 28$ ) and all but one defoliated plant sent up a new shoot in the 1999 growing season. For all plants ( $n = 59$ ), the estimated mean biomass all was  $551 \pm 31$  (SE) mg in 1998, and  $375 \pm 18$  mg in 1999. The estimated biomass of individual plants was positively correlated over these two periods (Fig. 1).

Principal components analysis indicated leaf area, sepal area, and stem diameter all had large ( $\geq 0.948$ ) positive loadings on the first axis. The first axis explained 91.1% of the variation in these morphological traits. Leaf height was significantly correlated with this axis ( $df = 52$ ;  $r = 0.61$ ;  $P < 0.0001$ ), indicating that it provides a fair index of plant size.

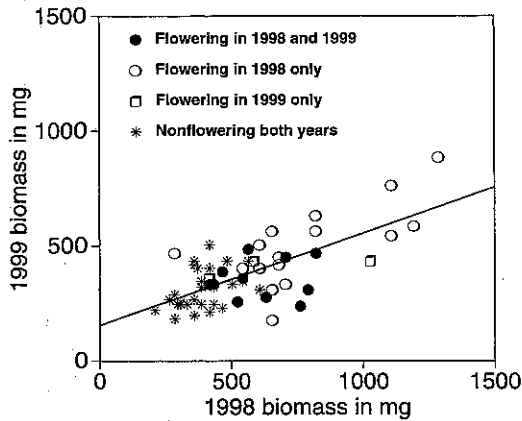


FIG. 1. The relationship between plant biomass in 1998 and 1999, in mg ( $n = 59$ ; Pearson  $r = 0.70$ ;  $P < 0.0001$ ). Solid circles indicate plants that flowered in both 1998 and 1999. Open circles represent plants that flowered in 1998, but not 1999. Open squares represent plants that did not flower in 1998, but did flower in 1999. Asterisks represent plants that flowered neither in 1998, nor in 1999.

Logistic regression indicated the defoliation in 1998 had no effect on flowering in 1999 ( $df = 1$ ; model  $\chi^2 = 0.30$ ;  $P = 0.59$ ). No plants with leaves  $< 20$  cm above the ground in 1998 flowered in 1999, and 65.9% of those plants with leaf heights  $> 20$  cm did not flower. Still, the odds of flowering in 1999 increased significantly with the natural log of leaf height in 1998 ( $df = 1$ ; model  $\chi^2 = 4.20$ ;  $P = 0.04$ ).

There was a significant negative relationship between the proportion of aboveground biomass in leaves and leaf height (Fig. 2). This indicates

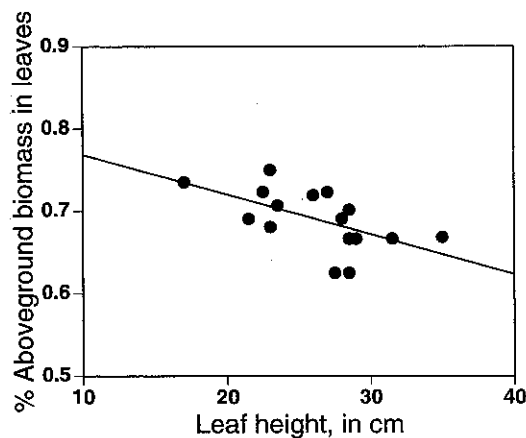


FIG. 2. The relationship between the proportion of aboveground biomass allocated to leaf tissue and leaf height, in cm.  $Y = 0.82 - 0.005 X$  ( $df = 14$ ;  $r^2 = 0.34$ ;  $P = 0.019$ ).

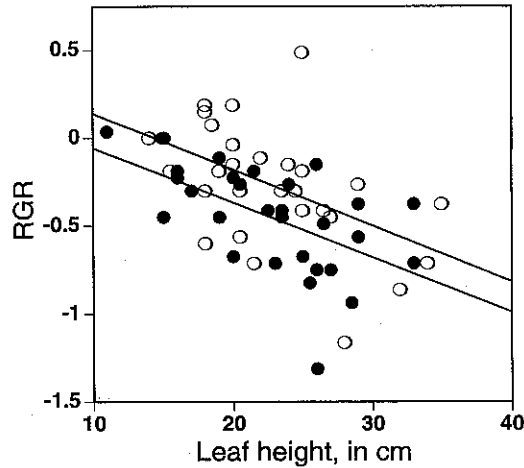


FIG. 3. The relationship between leaf height in 1998 and relative growth rate (RGR) over the 1998–1999 interval. Open circles represent control plants, and solid circles represent defoliated plants. Both the treatment ( $df = 1$ ;  $SS = 0.444$ ;  $F = 6.62$ ;  $P = 0.013$ ) and the covariate ( $df = 1$ ;  $SS = 2.171$ ;  $F = 32.35$ ;  $P < 0.001$ ) were significant but not their interaction.

taller plants must invest proportionately more biomass in stem structure and proportionately less biomass in leaves than shorter plants, as predicted (Givnish 1982). One way ANCOVA revealed that both defoliation and leaf height significantly reduced RGR (Fig. 3). These two variables explain 41.8% of the variation in the data. Some of this variation was due to differences in plant growth among sites. Two-way ANCOVA indicated defoliation, site, defoliation  $\times$  site, and leaf height all had significant effects on *Trillium grandiflorum* RGR (Table 2). This model including site effects explained over 70% of the variation in RGR.

Table 2. Two-way ANCOVA showing variables significantly affecting relative growth rates (RGR) of individual *Trillium grandiflorum* plants over the 1998–99 interval. Leaf height in 1998 is the covariate. Height  $\times$  site and height  $\times$  defoliation interactions were not significant, and were not included in the analysis. RGR at a single site was significantly lower than RGR at all other sites ( $df = 3,55$ ;  $F = 5.63$ ;  $P = 0.002$ ). This model explains 71.7% of the observed variation in RGR.

Variable	df	SS	F	P
Defoliation	1	0.151	4.27	0.044
Site	3	1.657	15.11	$< 0.001$
Defoliation $\times$ site	3	0.124	3.38	0.025
ln leaf height in 1998	1	2.093	57.27	$< 0.001$
Error	50	1.827		

**Discussion.** Plant size declined in both defoliated and control intact groups between 1998 and 1999. However, this is not unusual for perennial forest herbs which can show marked changes in size from one year to the next (Bierzuchudek 1982). It is possible that the poor growth of plants could be explained by the drier than normal climate during the growing season in 1998. The six month Standardized Precipitation Index indicates that northern Wisconsin experienced moderate drought conditions during that period (Edwards and McKee 1997; <http://enso.unl.edu/ndmc/watch/sep98spi.htm>). Because a drought can decrease whole plant stomatal conductance and hence net carbon assimilation, the drier than normal conditions could account for the decline in plant size between the two periods.

As predicted, defoliated plants had lower RGR than control plants. Lubbers and Lechowicz (1989) also found that the density and the total photoassimilate content of *Trillium grandiflorum* rhizomes declined following partial defoliation. Similarly, *Trillium* plants protected from deer browsing are usually larger than unprotected plants (Anderson 1994; Augustine and Frelich 1998). Because defoliation has an immediate and lasting effect on plant growth, these differences in size can emerge after just a year or two once an enclosure is erected in an environment with moderate to high browsing pressure. It is less clear how quickly *Trillium* plants and populations may be able to rebound once deer densities decline.

Despite its effect on growth, defoliation did not appear to reduce reproduction in the following year. Augustine and Frelich (1998) found a similar pattern in *T. grandiflorum* in Minnesota. These results should not be extrapolated to other species of forest herbs, though. In her work on *Aralia nudicalis*, Edwards (1985) found that defoliation significantly reduced the probability of reproduction the following year. Experimental defoliation of *Tipularia discolor* resulted in complete reproductive failure for 2 years following defoliation (Whigham 1990). Nor should the short-term impacts of defoliation be extrapolated to longer time spans (Doak 1992). The proportion of flowering *T. grandiflorum* plants in a population declines as deer densities increase, and defoliation over multiple seasons clearly depresses reproduction (Anderson 1994).

While some plants from grassland or desert habitats undergo overcompensatory growth in response to defoliation (McNaughton 1983,

1986; Paige 1992), it is unlikely that perennial forest herbs can do so (Table 1). This difference in compensatory abilities may be due in part to the characteristic differences between sun-adapted and shade-adapted plants (Givnish 1988; Whitham et al. 1991). At the leaf level, sun-adapted plants have higher concentrations of Rubisco (ribulose 1,5-biphosphate carboxylase—the enzyme responsible for fixing carbon) in their leaves and thus a higher potential photosynthetic rate than shade-adapted plants. The higher concentration of leaf nitrogen found in sun plants should make plants more attractive to herbivores. Higher nitrogen concentrations in leaves also favor quantitative, carbon-based defenses, such as tannins and phenols (Coley et al. 1985; Givnish 1988). Overcompensatory growth could also be a carbon-based adaptation to herbivores: instead of using carbon-based defensive compounds, plants could store photoassimilates in roots until herbivores attack. These reserves could then be mobilized to construct new leaves and flowers. In contrast, shade-adapted species tend to have lower nitrogen concentrations in leaves and to favor qualitative, nitrogen-based defensive compounds like alkaloids (Givnish 1988). Shade plants may also employ more conservative and determinant growth strategies such as preformed buds that prevent them from quickly mobilizing stored reserves (Waller 1986, 1988).

As plant size increased, RGR declined over the 1998–99 interval. This is common pattern in plants that presumably reflects the fact that larger plants have lower mass-specific photosynthetic rates than smaller plants (Givnish 1982). *Trillium grandiflorum* inhabits mesic habitats, where herbaceous cover is dense relative to drier, less fertile sites. In mesic environments, optimal plant leaf height reflects a trade-off between competitive ability (taller plants intercept more light, thus making it unavailable for neighbors) and biomechanical stability (Givnish 1982). Environmental variation affecting RGR can create conditions whereby individual plants exceed or fall short of this optimum.

Both ANCOVAs indicate that RGR declines in response to defoliation and higher leaf placement. Partitioning the variance revealed that leaf height explains almost 5 times more of the variance in RGR (34.1%) than does defoliation (7.0%) in the one-way ANCOVA. These differences are mirrored in the two-way ANCOVA where leaf height explains 35.8% of the variation in RGR, whereas defoliation and the defo-

liation x site interaction together only explain 4.7% of the variation in RGR. Residual unexplained variation in RGR may reflect fine-scale environmental variation or genetic differences among plants. While the heritability of RGR in *Trillium grandiflorum* has not been studied, research on *Viola sororia* suggests that significant differences in RGR can occur among genets (Antlfinger et al. 1985). Additional variation could also reflect differences in the defoliation history of individual plants. For example, a plant that was defoliated in the year prior to our study may grow less than a neighboring plant that was not defoliated. The weak relationship between leaf height in one season and flowering in the next might also reflect differences in genetics and plant history.

When faced with a choice, deer tend to select larger *T. grandiflorum* plants over smaller ones (Rooney 2000). This has two consequences. Because only the largest plants flower (Hanzawa and Kalisz 1993; Augustine and Frelich 1998), deer tend to consume a disproportionate number of flowering plants, preventing reproduction in that year. Additionally, herbivory tends to reduce a plant's size in the next year. This can reduce the plant's ability to compete for light in the short-term, may reduce lifetime reproductive success in the long-term.

We found that RGR declined in response to both defoliation and increasing leaf height. Defoliation did not affect the likelihood of emergence or flowering the next season, however. These relationships suggest that the decline in mean *Trillium* plant size observed in populations of higher deer density (Anderson 1994; Augustine and Frelich 1998) may reflect reductions in the RGR of individual plants more than the mortality of grazed plants (at least initially). While deer impacts seem likely to significantly depress lifetime fitness in *Trillium grandiflorum* populations, we have yet to assess the long-term impacts of deer grazing on population growth. Further experiments employing exclosures, monitoring, and/or multi-year defoliation treatments are therefore needed to assess what deer impacts and densities are compatible with maintaining this and other sensitive forest understory species.

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