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# Timing of defoliation and its effect on bud development, starch reserves, and sap sugar concentration in sugar maple

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Sapling sugar maple (*Acer saccharum* Marsh.) trees were defoliated artificially at 10-day intervals beginning May 27 and ending August 5, 1981. Refoliation, terminal bud and shoot development, and xylem starch and sap sugar concentration were observed in defoliated and control trees. All defoliated trees refoliated, but decreasingly with later defoliation. Defoliation caused an acceleration in the rate of primordia initiation in terminal shoot apices. After early season defoliations, the developing buds in the axils of the removed leaves abscissed, but axillary and terminal buds on the refoliated terminal shoots survived through winter. In late season defoliation, most buds of refoliated shoots did not survive and the next year's growth depended on axillary buds formed prior to defoliation. Thus, when progressing from early to late defoliations, the next year's shoot. Early October starch concentration in xylem decreased with later defoliation and was nearly absent in shoots and roots of trees defoliated in late July. There was not, however, a corresponding decrease in sap sugar concentration. Mortality occurred only in late defoliated trees and was associated with starch depletion.

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Des gaules d'érable à sucre (*Acer saccharum* Marsh.) ont été défoliées artificiellement à intervalles de 10 jours commençant le 27 mai et se terminant le 5 août 1981. Sur des arbres défoliés et des arbres témoins on a suivi la refeuillaison, le développement du bourgeon terminal et de la pousse, ainsi que la concentration en amidon et en sucres du xylème. Tous les arbres défoliés ont refeuillé, mais d'une façon décroissante avec le retard de la défoliation. La défoliation a causé une accélération dans le taux d'initiation des primordia de l'apex des pousses terminales. Après les défoliations en début de saison, les bourgeons se développant dans les aisselles des feuilles enlevées sont tombés mais les bourgeons axillaires et terminaux sur les pousses terminales refeuillées ont survécu à l'hiver. Dans le cas des défoliation tardives, la plupart des bourgeons des pousses refeuillées n'ont pas survécu, et la croissance de l'année suivante s'est faite à partir des bourgeons axillaires formés avant la défoliation. Ainsi, en progressant d'une défoliation nâtive à une défoliation tardive, la croissance de la pousse suivante dépendait moins des portions formées tardivement de la pousse de l'année précédente, et davantage des portions formées initialement. La concentration en amidon du xylème au début d'octobre allait décroissante avec le retard des défoliations et elle était presque nulle dans les pousses et les racines des arbres défoliés à la fin de juillet. Cependant, on n'a pas observe de réduction correspondante de la concentration en sucre de la sève. La mortalité s'est produite seulement chez les arbres défoliés tardivement et elle était reliée à un épuisement de l'amidon.

## [Traduit par le journal]

#### Introduction

Defoliated trees that refoliate have fewer and smaller leaves (Heichel and Turner 1976; Wargo 1981a), store less food (Staley 1965; Wargo et al. 1972; Wargo 1981a), grow less, and die back and decline (Giese et al. 1964; Houston and Kuntz 1964; Staley 1965; Wargo 1981b). These effects have been observed to depend on the severity, frequency, and timing (when during the growing season) of defoliation, as well as the condition of the trees when defoliated and growing conditions after defoliation (Wargo 1978, 1981a, 1981b). The disruption of developmental events caused by defoliation, including bud and embryonic shoot growth, must influence subsequent dieback and decline. For example, dieback of branches on defoliated trees during the dormant season may occur because buds that formed during the shortened growing season after refoliation are immature and the twigs have insufficient carbohydrate for respiration; early season defoliators may have less of an effect because new buds have a longer time to form and are mature. However, little has been done to document these

hypotheses. In this paper, we report the effects of sugar maple defoliation at successively later dates in the growing season on subsequent bud and embryonic shoot development, starch reserves, and sap sugar concentrations.

# Materials and methods

# Bud development

We selected one hundred twenty 7-year-old sugar maple (*Acer* saccharum Marsh.) saplings from about 300 growing in a nursery bed at the Vermont Department of Forests, Parks, and Recreation Nursery at Essex Junction, Vermont. The trees were spaced at about 1.2-m intervals in several rows that were about 2 m apart. Selected trees were numbered randomly and divided into five groups of 24 each. One group (B) was sampled sequentially in 1981 to determine bud development at the time of defoliation. Two groups (D1 and D2) were defoliated; D1 was sampled in autumn 1981 and D2 was sampled in spring 1982 after a single defoliation. The remaining two groups (C1 and C2) were control trees; C1 was sampled at the same time as D1 and C2 was sampled at the same time as D2.

There were eight defoliation dates during the 1981 growing season occurring at 10-day intervals beginning May 27 and ending August 5.

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On each date, three trees randomly selected from among each of two groups (D1 and D2) were defoliated completely by excising the leaves at the distal end of the petiole; at the same time, 1981 shoots were excised from three randomly selected trees from group B. Three long (Epf long; see Gregory 1980) and three short shoots were taken from each of the B trees. No heterophyllous shoots were sampled because a frost in late spring had damaged many of the uppermost vigorous shoots. The number and type of apical dome derivative (undifferentiated primordia, scales, embryonic leaves) that had been produced in the developing bud at the terminal shoot apex and the number and midrib length of leaf pairs of the 1981 shoots were recorded for each of the excised long and short shoots. The same information was recorded for the D1 and C1 trees at the end of the 1981 growing season (October 5) and for the D2 and C2 trees early in the next growing season (June 7, 1982). The D2 trees were then divided into two groups: D2a (those defoliated on May 27 through June 26, 1981) and D2b (those defoliated after June 26, 1981). The D2a trees were defoliated again on June 9, 1982, and the D2b trees were defoliated at the relatively late seasonal date of July 29, 1982. Final measurements and observations were made during the 1983 growing season to determine the general condition and mortality of the D2a and D2b trees.

Personnel of the Vermont Department of Forests, Parks, and Recreation supplied us with samples from mature sugar maple trees collected in October 1981 from four natural stands in Vermont that were undefoliated or defoliated by either the forest tent caterpillar (*Malacosoma disstria*) or saddled prominent (*Heterocampa guttivitta*) in the 1981 growing season. We counted the apical dome derivatives, as before, that had been produced in the developing buds of terminal shoot apices of Epf long and short roots in undefoliated, defoliated, and refoliated branches.

We determined the pattern of sap sugar concentration as a function of time of the year for a large, mature, open-grown sugar maple (Fig. 8) at the Essex nursery site. Three shoots containing all of the 1- and 2-year-old secondary xylem were excised from the outer, lower crown at about biweekly intervals from October 6, 1981, through March 1, 1982, and then at weekly or shorter intervals thereafter through May 24, when the new leaves were fully expanded. Extracted sap from the three shoots was combined and the concentration of soluble sugar was determined as described previously (Gregory and Hawley 1983). During the same period, sap was extracted and analyzed in the same way from the young, nursery-grown trees at biweekly intervals. Three defoliated (D1) and six control trees were tested each sampling date. On March 31, 1983, all of the live D2 and 19 of the C2 trees were similarly sampled for sap analysis. The Vermont Department of Forests, Parks, and Recreation also supplied us with refractometer readings of sap from a Vermont sugar bush. As shown previously (Gregory and Hawley 1983), refractometer readings closely approximate percent sap sugar concentration.

To verify the effects of defoliation on starch content, two 7-year-old saplings, each growing in a crowded nursery bed, were defoliated on each of the following dates: June 3, July 15, and July 29, 1983. On October 6, 1983, we removed cross sections from the upper shoots and from lateral roots of one of the trees defoliated on each of the dates cited and from two adjacent undefoliated trees. The samples were fixed in Navashin's fluid, dehydrated and embedded in parafin, sectioned at 20  $\mu$ m thickness, and stained by the periodic acid – Schiff's reaction. The sites and relative quantity of starch in the storage tissues of the secondary xylem were recorded photomicrographically. Additional secondary xylem cross sections from the upper shoot and a lateral root were collected for quantitative starch analysis. Extraction, hydrolysis, and glucose assay were done according to Hassig and Dickson (1979). Standard starch solutions were prepared from Baker reagent-grade potato starch.

#### Results

# Refoliation

In early defoliations (before mid-June), most of the developing terminal buds of all shoot types flushed, while most of the developing axillary buds did not. Rather than developing further after defoliation, the latter usually abscissed along with the subtending defoliated petioles about 2 weeks after defoliation when the terminal apices were beginning to flush. Hence, there was little or no foliage produced the following year on that part of the shoot formed between vernal budbreak and defoliation in the year of defoliation (Fig. 1). Although the number of leaf pairs on the shoots refoliating after early defoliations usually was comparable to what had existed on the subtending shoots prior to defoliation, the internodes were shorter and the leaves were noticeably smaller than on the control trees. The basal leaf pairs usually were small and had incompletely developed margins and lobes, suggesting that the primordia from which they developed may have begun to differentiate into scales at the time of defoliation. It required about 1 month for the new foliage of these early defoliated trees to fully expand.

As the defoliation dates advanced, fewer of the developing buds foliated and these were confined increasingly to the more vigorous Epf long and heterophyllous shoots. The leaves became smaller and often were not fully formed. In the later defoliations, the axillary buds of the first-formed current shoots, that portion of the current year's shoots formed prior to defoliation, did not abscise as in earlier defoliations. On the other hand, fewer of the buds on the last-formed shoots survived the winter; the most distal buds, the ones formed last, often did not foliate the next spring (Fig. 2).

Refoliation of trees defoliated in late July was confined almost entirely to the terminal buds of vigorous secondary branches and most of the late formed shoots did not survive (Fig. 3). Nearly all new shoot growth the following year was from axillary buds on that part of the shoot formed before defoliation.

Thus, when progressing from early to late defoliation, we observed that the next year's shoot growth depended decreasingly on the last-formed and increasingly on the first-formed portions of the previous year's shoot.

There was some mortality, but only among those trees defoliated very late in the growing season. Two of the six trees defoliated on August 5, 1981, failed to foliate the following spring and were dead when next observed in early June. Three of these remaining four trees were defoliated again on July 29, 1982, along with the other trees previously defoliated after June 26, 1981. Again, mortality was confined to the trees first defoliated on August 5, 1981; two of these three trees died following the second defoliation, while all others survived through the next (1983) growing season.

#### Bud and leaf development

There was no difference in rate of primordia initiation for long and short shoots at the beginning of the season. After early June, however, the rate of primordia initiation declined markedly for short shoots (Figs. 4 and 5). By the end of July, plastochron duration (PD) for short shoots was about 30 days, indicating that primordia initiation for the season was almost over; that is, only one pair of primordia would be initiated (Fig. 5). The abrupt decline in rate for long shoots did not begin until early July (about day 190) and PD reached 30 days in mid-August (about day 230), 2–3 weeks later than in short shoots (Fig. 5).

Defoliation followed by refoliation caused a marked increase in the rate of primordia initiation by the apices in both long and short shoots (Fig. 6). The mean number of plastochrons that occurred after each of the 1981 defoliation dates for control and defoliated trees was the difference between the mean number of 1981 primordia that had been produced by the shoot apices at the time of defoliation (from B1 trees) and the mean number at the



FIG. 1–3. Heterophyllous shoots in May 1984 from trees defoliated (1) June 6, (2) July 15, and (3) July 29, 1983. Arrows show the position of developing terminal buds at the time of defoliation.



FIG. 4. Number of primordia pairs initiated by terminal shoot apices ( $\bigcirc$ , long;  $\bigcirc$ , short) of control trees in 1981 as a function of time (day number or calendar date). Each point represents a mean value calculated from nine shoot apices. Polynomial equations fitted to these data points are as follows: long,  $y = 19.1 - 0.453X + 0.0036X^2 - 0.0000074X^3$ ; short,  $y = 42.8 + 0.559X - 0.0018X^2 + 0.0000017X^3$ .

end of that season (from C1 and D1 trees). From four to eight more pairs of primordia were initiated by the apices of the defoliated trees compared with control trees during 1981 and the greatest acceleration occurred in late June (Fig. 7). Even after the last defoliation on August 5 (day 217), when primordia initiation for the season was normally ending, the apices of the defoliated trees were able to increase their rate of activity enough to produce rudimentary buds consisting of four to five scale pairs and one to two pairs of undifferentiated primordia (Table 1).

The number of bud scales in both shoot types declined steadily with later defoliation dates (Table 1). Embryonic leaf production was unaffected by defoliations in late May and throughout June, but their numbers were much reduced by later defoliations and trees defoliated after late July (day 207) had no embryonic leaves.

In the late spring of the year following defoliation (1982), after the new foliage was fully expanded, all the surviving trees appeared similar and were not distinguishable from controls by cursory inspection. Closer examination revealed some of the characteristics described under *Refoliation* and that leaf size and mean midrib length declined as a function of the lateness of the defoliation date, especially for the short shoots (Table 2). The ability of the shoot apices to recover from the effects of the previous year's defoliation was apparent from the status of the developing terminal buds. Only those trees defoliated in midseason (July 6 and 16, 1981) had produced significantly



FIG. 5. Plastochron duration, the reciprocal of the first derivative of the polynomial equations in Fig. 4, of control trees in 1981 as a function of time. ----, short shoots; —, long shoots.

fewer bud primordia than the controls and even then the developmental difference was equivalent to only about one plastochron (Table 3).

Leaves of defoliated trees were also smaller in 1983, after a second defoliation in 1982, especially those defoliated in late July (Table 4). There were no differences in the accumulated number of initiated primordia between twice-defoliated and control trees, but there were not any midseason defoliations in 1982.

Bud development in mature trees in natural stands defoliated by insects (Table 5) was similar to that in the nursery-grown saplings (Table 1). There was not much place to place difference in the number of terminal bud constituents in undefoliated shoots. Defoliated but unrefoliated shoots were similar to the undefoliated shoots. In the trees defoliated by the forest tent caterpillar (an early season defoliator), the number of terminal bud constituents in shoots that refoliated paralleled that of the nursery saplings defoliated in early to mid-June; in the trees defoliated by the saddled prominent (a late season defoliator), bud development corresponded approximately to the mid-July nursery defoliations.

### Stored starch

We observed the concentration of starch histochemically and chemically in shoot and root xylem of sapling trees defoliated June 3, July 15, and July 29, 1983. Concentration decreased with later defoliations (Table 6). There was no histochemically detectable starch in early fall in the root samples of a tree defoliated July 29 and only a small amount in the outer xylem of shoots of the same tree.

A concern that we had with respect to the integrity of our results was that the treatment effect in defoliated trees might be ameliorated by translocation of reserves from control to treatment trees via natural root grafts. Although we cannot exclude the possibility of such grafting, the effect, with respect to starch reserves, was not apparent. Further, any replenishment of carbohydrate because of root grafting probably would be more evident in these trees since they had developed from an



FIG. 6. Number of plastochrons in the shoot apices of defoliated (short shoots,  $\textcircled{\bullet}$ ; long shoots,  $\blacksquare$ ) and control (short shoots,  $\bigcirc$ ; long shoots,  $\Box$ ) trees after each 1981 defoliation date as a function of time. Each point represents a mean value calculated from nine shoot apices. Polynomial equations fitted to these data points were as follows:  $\textcircled{\bullet}$ ,  $y = 46.2 - 0.35X + 0.000655X^2$ ;  $\bigcirc$ ,  $y = 29.1 + 0.57X - 0.00188X^2$ ;  $\blacksquare$ ,  $y = 51.7 - 0.46X + 0.00103X^2$ ;  $\square$ ,  $y = 10.6 + 0.09X - 0.00053X^2$ .

overstocked nursery bed and were growing very close together, much closer than the other trees used in this study.

#### Sap sugar

The typical pattern of sap sugar concentration for sugar maple during fall, winter, and spring was observed in the large, open-grown tree at the nursery site (Fig. 8). There was a steady increase in sap sugar during the fall coincident with the combination of relatively low night and high day temperatures. When winter temperatures were consistently below freezing, the increase in sap sugar concentration ceased. In early spring,

 TABLE 1. Terminal bud constituents of long (L) and short (S) shoots at the end of the

 1981 growing season (Oct. 6) for control trees and for trees defoliated progressively

 later in the growing season

1981	Scales		Embryo	nic leaves	Undifferentiated primordia	
defoliation date	L	S	L	S	L	S
Control	11.6±0.1	9.6±0.2	2.8±0.1	$2.2 \pm 0.1$	1.2±0.0	1.1±0.0
May 27	9.3±0.5	$8.2 \pm 0.8$	$2.1 \pm 0.3$	$2.1 \pm 0.3$	1.8±0.3	$1.1 \pm 0.3$
June 6	7.7±0.5	8.3±0.5	$2.5 \pm 0.6$	$2.2 \pm 0.4$	$1.5 \pm 0.6$	$1.7 \pm 0.5$
June 16	$7.8 \pm 0.6$	$7.2 \pm 0.3$	$2.5 \pm 0.4$	$2.1 \pm 0.3$	$1.0 \pm 0.4$	$0.8 \pm 0.3$
June 26	$8.2 \pm 0.6$	$7.6 \pm 0.5$	$2.2 \pm 0.4$	$1.6 \pm 0.5$	$1.1 \pm 0.3$	$1.3 \pm 0.4$
Julv 6	$6.6 \pm 0.6$	$6.0 \pm 0.8$	$1.3 \pm 0.4$	$0.9 \pm 0.4$	$1.4 \pm 0.6$	$1.3 \pm 0.4$
July 16	$7.0 \pm 0.5$	$6.2 \pm 0.5$	$1.3 \pm 0.5$	$0.8 \pm 0.5$	$1.4 \pm 0.4$	$1.4 \pm 0.4$
July 26	6.4±0.6	$5.5 \pm 1.1$	0.0	0.0	$1.6 \pm 0.4$	$1.6 \pm 0.5$
August 5	5.3±0.8	$4.8 \pm 0.8$	0.0	0.0	$1.2 \pm 0.3$	$1.0 \pm 0.0$

NOTE: Values represent the number of pairs of each constituent and are means  $\pm$  sampling errors (at p = 0.05).



FIG. 7. The increase in plastochrons in defoliated shoot apices (---, short; —, long) of defoliated trees as a function of time. The curves represent the difference between the curves of defoliated and control trees in Fig. 6 as calculated from the polynomial equations.

when daytime temperatures began to consistently exceed freezing, the concentration of sugars again increased, reaching a maximum in early April. As the weather warmed and freezing night temperatures no longer occurred, sap sugar declined rapidly. By the time the new foliage was fully expanded in late May, sap sugars were barely detectable. Throughout this entire period almost all the soluble sugar (> 95%) was sucrose.

We simultaneously extracted sap and measured sap sugars in the saplings from the defoliation study. There was no significant difference (p = 0.05) in mean sap sugar concentration between defoliated (1.19% sucrose) and control (1.29% sucrose) trees in the fall-winter-spring period of 1981-1982 following the 1st year of defoliation. Trees defoliated for the second time early the next year (June 9, 1982) had small but significantly higher concentrations of sap sugar (2.8%) than undefoliated controls (2.4%) in early spring, 1983, while trees defoliated for the



FIG. 8. Soluble sap sugars of an open-grown sugar maple and daily maximum and minimum temperatures as a function of time, 1981–1982.

second time late in the growing season (July 29) had slightly but not significantly higher concentrations of sap sugar (2.6%).

Data from mature, natural sugar maple stands indicate that natural defoliation by insects reduced sugar concentration in sap collected the following spring. One of two adjacent sugar bush areas (2300 tapholes), in a stand heavily defoliated by the forest tent caterpillar, was protected from defoliation in 1980 by

TABLE 2. Length (millimetres) of midrib of leaves from the first two nodes of long (L) and short (S) shoots in 1982 after defoliation in 1981

1981	No	ode 1	Node 2		
date	L	S	L	S	
Control	112±3	99±3	118±3	89±3	
May 27	$129 \pm 12$	$100 \pm 10$	$125 \pm 11$	$94 \pm 10$	
June 6	113±5	$92 \pm 8$	$111 \pm 8$	$88 \pm 7$	
June 16	$101 \pm 7^{**}$	83±9**	99±7**	81±7*	
June 26	110±8	87±7**	111±6	83±6	
July 6	110±7	88±10**	107±8*	80±6*	
July 16	112±9	69±7**	98±7**	57±7**	
July 26	89±5**	75±5**	96±6**	67±6**	
August 5 <sup>b</sup>					

NOTE: Values are means  $\pm$  sampling errors (at p = 0.05).\*,mean value significantly different from control at p = 0.05; \*\*, mean value significantly different from control at p = 0.01.

<sup>b</sup> High winter mortality; sample size was too small to calculate reliable means.

TABLE 3. Total number of initiated primordia pairs in developing terminal buds in long (L) and short (S) shoots by June 7 and 8, 1982, as a function of 1981 defoliation date

1981 defoliation date	L	S
Control	8.0±0.2	7.8±0.1
May 27	$8.0 \pm 0.4$	7.6±0.4
June 6	$8.0 \pm 0.4$	$7.6 \pm 0.4$
June 16	$7.8 \pm 0.3$	$7.8 \pm 0.6$
June 26	$7.2 \pm 0.6$	$7.6 \pm 0.4$
July 6	6.9±0.6*	6.4±0.4*
July 16	6.8±0.3*	6.6±0.4*
July 26	$7.4 \pm 0.4$	7.4±0.4
August 5 <sup>b</sup>		

NOTE: Values are means  $\pm$  sampling errors (at p = 0.05).

\*, mean value significantly different from control at p = 0.05.

<sup>b</sup> High winter mortality; sample size was too small to calculate reliable means.

 TABLE 4. Length (millimetres) of midrib of leaves on the first two

 nodes of long (L) and short (S) shoots in 1983 after early or late season

 defoliations in 1981 and 1982

D.f.listian	No	de 1	Node 2		
date	L	S	L	S	
Control Early <sup>a</sup> Late <sup>b</sup>	128±4 120±5 96±5	101±4 96±4 76±4	127±5 120±4 97±5	90±4  89±4  71±4	

Notes: Values are means  $\pm$  sampling errors (at p = 0.05). Mean values within shoot types connected by vertical lines are not significantly different at p = 0.05 (LSD multiple comparisons). All other values within shoot types are significantly different at p = 0.05. The foliated May 27 to June 26, 1981, and June 9, 1982.

<sup>b</sup>Defoliated July 16 to August 5, 1981, and July 29, 1982.

spraying. The other unprotected area (3200 tapholes) was defoliated that year. Both areas were protected by spraying in 1981. Refractometer readings of sap entering the sugarhouse from the two areas by way of separate tubing systems showed slightly but significantly lower values for the defoliated area (Table 5).

# Discussion

Defoliation clearly caused an acceleration in the rate of primordia initiation in the terminal buds of the defoliated shoots that refoliated. This acceleration apparently allowed for sufficient development in refoliated shoots after early season defoliation (May and June) for the buds to survive through the winter. In late defoliations, however, most terminal buds of refoliated shoots did not survive. When bud scales were reduced to about six pairs or fewer and when there was little or no embryonic shoot development, the buds and associated shoot tissue died.

Thus, sugar maple seems to have different ways to maintain its shoot system after defoliation. If the defoliations are relatively early (late May, June), most buds flush and refoliation occurs. Although the axillary buds on the predefoliation part of the current year's shoot abscise after defoliation, there is enough remaining time in the growing season for new buds of the postdefoliation shoots to develop and survive. The ability of the apices to accelerate their rate of primordia initiation is a key factor in this survival mechanism. In the later defoliations (July and early August), only the distal buds on the most vigorous shoots flush and refoliate. These postdefoliation shoots are less likely to survive the winter. However, the axillary buds of the predefoliated part of the current year's shoot, which are well along their developmental pathway at the time of defoliation, do not abscise; they survive the winter and foliate the following spring. There is probably a middle period (late June, early July) when a combination of these mechanisms occur. Defoliations after early August have been shown to have much less effect than earlier defoliations, primarily because the trees do not refoliate (Wargo 1981b).

Another compensating mechanism may be photosynthetic enhancement in regrowth foliage. In Connecticut, young red maple trees that were completely defoliated in mid-June, had a rate of net photosynthesis in leaves of the refoliated crown from mid-July through September that was about 50% higher than in primary foliage of undefoliated trees (Heichel and Turner 1983). This was attributed directly to elevated CO<sub>2</sub> assimilation, a function of greater nitrogen concentration and cellular activity (respiration) in regrowth foliage. Yet despite the photosynthetic enhancement, Heichel and Turner (1983) calculated that net assimilation after refoliation decreased because of a considerable reduction in total leaf area after refoliation; the calculated daily carbon budget for leaf canopies of refoliated red maple was 57% of undefoliated controls. In our studies, we noted but did not quantitatively record decreasing refoliation with later defoliation. Hence, the quantities of carbon fixed per unit of time per tree presumably would decrease with later defoliations.

It seems, therefore, that young, healthy sugar maple trees growing on good sites can survive defoliation at most times during the growing season, even when defoliations are repeated in successive years. Earlier studies substantiate this (Parker and Houston 1971; Heichel and Turner 1976).

We know, however, that mortality sometimes occurs after defoliation. In this study, several of the late defoliated trees died and this mortality seemed related to starch depletion. The effects of defoliation, including mortality, on young sugar maple trees growing in an abandoned field in southern Connecticut, were more severe in mid-June than in May, July, or August defoliated trees, and the autumn starch levels were most depleted in the roots of the June defoliated trees (Wargo 1981*a*, 1981*b*). Thus, in both studies, the most severe effects of defoliation were associated with low autumn starch levels, but

Stand	Defoliator	Shoot condition <sup>a</sup>	Shoot type	n	Scales	Embryonic leaves	Undifferentiated primorida
1	FTC	UR R	L L	10 9	11.5±0.8 7.9±0.5	3.0±0.0 2.8±0.3	1.0±0.0 1.0±0.0
2	SP	UD	L S	30 41	$10.2 \pm 0.5$ 9 4 ± 0 3	$3.0\pm0.1$	$1.0\pm0.0$
		UR	L S	22 45	$10.3 \pm 0.6$ 10.9 ± 0.5	$2.6\pm0.3$ 2.6±0.3	$1.3\pm0.2$ 1.3±0.1
		R	L S	39 45	$5.1\pm0.2$ $4.6\pm0.2$	$0.1\pm0.2$ $0.1\pm0.1$	$1.2\pm0.1$ $1.2\pm0.1$ $1.2\pm0.1$
3	SP	UD	L	15 14	$11.1 \pm 0.5$	$3.1\pm0.1$	$1.1 \pm 0.1$
		UR	L	14 10 15	$10.8 \pm 0.5$ $11.1 \pm 0.6$ $10.3 \pm 0.7$	$2.8 \pm 0.2$ $3.0 \pm 0.0$ $3.0 \pm 0.0$	$1.0\pm0.0$ $1.0\pm0.0$
		R	L S	15 15 15	$5.1\pm0.5$ $5.1\pm0.6$	$1.6\pm0.3$ $1.3\pm0.2$	$1.0\pm0.0$ $1.1\pm0.2$ $1.1\pm0.2$
4	SP	UR	L S	13 17	$10.2 \pm 0.5$ $10.4 \pm 0.4$	$2.4\pm0.4$ $2.1\pm0.3$	$1.0\pm0.0$ $1.0\pm0.0$
		R	L S	10 10	$4.3 \pm 0.4$ $4.0 \pm 0.8$	$0.6\pm0.4$ $0.4\pm0.4$	$1.5\pm0.4$ $1.8\pm0.3$

TABLE 5. Number of terminal bud constituents in long (L) and short (S) shoots in October 1981 in natural sugar maple stands defoliated by forest tent caterpillar (FTC) or saddled prominent (SP) in 1981

Note: Values represent the number of pairs of each constituent and are means  $\pm$  sampling errors (at p = 0.05).

"UD, undefoliated shoots; UR, defoliated shoots that did not refoliate; R, defoliated shoots that refoliated.

TABLE 6. Autumn starch content (milligrams per gram dry weight) in shoot and root xylem of undefoliated and defoliated trees

1983 defoliation date	Shoot	Root
Control	13.5	35.1
June 6	13.2	34.1
July 15	10.9	20.6
July 29	3.7	0.3

the timing of the defoliations that promoted this effect was markedly different.

There were two important differences between the Connecticut and Vermont defoliation experiments. The Vermont trees were growing on more fertile nursery soils that probably did not contain the root rot fungus Armillaria, a pathogen that is ubiquitous in forest soils and there were no late July or early August defoliations in Connecticut. The latter were most devastating for the Vermont trees with respect to unreplenished carbohydrate, much more than for the mid-July defoliation (Table 6). Trees defoliated after early August do not refoliate and thus retain much more of their carbohydrate reserves through fall and winter (Wargo 1981a, 1981b). An earlier study in southern Connecticut (Wargo 1979) on radial growth and starch storage in roots of sugar maple showed that maximum radial growth occurred during the period mid-July to mid-August. It is conceivable, therefore, that late July and early August defoliations might cause greater depletion of both shoot and root starch than defoliation at other times because of the combined demands of refoliation and root growth. The absence of mortality in the June defoliated Vermont trees may be due either to their more vigorous growth or to the lack of Armillaria

infection in roots of the stressed trees on the nursery site. The latter could be especially important with respect to carbohydrate depletion for it has been shown (Cooksey et al. 1983) that sucrose is an elicitor of phytoalexin production in plants. It is well established that carbohydrate reserves are immediately exhausted by refoliation after artificial defoliations in June (Riedl 1937; Wargo 1981a, 1981b). The timing of the defoliation-refoliation sequence did not appreciably affect the rate of primordia initiation in terminal shoot apices in the following years (Tables 3 and 5), though fully expanded leaves tended to be smaller than on control trees (Tables 2 and 4). Overall, the young, healthy trees used in this study were especially resilient in their response to and recovery from defoliations. Mortality occurred only in late treatments. Even 2 successive years of defoliation did not seem very detrimental to most trees in terms of their ability to recover.

In this study, the concentration of soluble sap sugars appeared to be independent of starch concentration in the secondary xylem and, therefore, not affected by defoliation. Even those defoliation—refoliations that caused severe autumn starch depletion did not reduce overwintering sap sugar concentrations. It apparently does not require much storage carbohydrate to attain the sap sugar concentrations normally found in sugar maple. Continued sap flow as in a commercial operation, however, might reduce the total pool of sugar, resulting eventually in a less than normal supply for efflux into vessel water. Data from the defoliated sugarbush presented here (Table 5) support this possibility.

Sap sugar concentration has been reported to be a function of the amount of ray tissue per unit of xylem (Morselli *et al.* 1978; Wallner and Gregory 1980). It was suggested that more ray tissue would provide greater storage space for starch and, hence, more soluble sugar to permeate into vessel water and, in addition, more ray to vessel contact (Gregory 1982). It now appears that the former is not plausible, given that low starch concentrations did not reduce sap sugar concentrations in this

study. It seems more likely that the positive relationships between the amount of ray tissue and sap sugar concentration might be a function of increased contact area between parenchyma cells and vessel segments. Sauter (1982) calculated that sucrose enters the vessels of Salix  $\times$  Smithiana at a maximum rate of 3-8 mg/mL of tracheal sap per 24 h at 21°C from December to March. This species, according to Sauter (1982), has almost no axial parenchyma bordering the vessels. Sauter (1982) calculated further that in other tree species such as sugar maple, in which the vessels are almost completely surrounded by parenchyma cells, the apparent permeation area is 4 times greater and comparable sucrose concentrations of the sap thus could be reached 4 times faster. We have found this to be a precise estimate in current experiments. In perfusion experiments with shoot segments of sugar maple collected in mid-March, when sap sugar concentrations are highest, we found that sucrose entered the vessels at a mean rate of 24 mg/mL of vessel water per 24 h at 20°C.

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