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Effects of Defoliation, Girdling, and Severing of Sugar Maple Trees on Root Starch and Sugar Levels



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ABSTRACT

Root starch levels of defoliated sugar maple trees, on the average, were lower after 4 weeks in two separate experiments than in girdled, cut off, or girdled and defoliated trees. Root starch levels in all these treatments were lower than in controls. Sucrose levels, but not the levels of fructose and glucose, followed the same trends. It is suggested that carbohydrates are moved upward in the phloem of the stem and to a lesser extent in the xylem in defoliated trees, and that this accounts for the relatively low levels of starch and sucrose in these trees' roots.

INTRODUCTION

DEFOLIATION of sugar maple (*Acer saccharum* Marsh.) trees would be expected to cause a decline in root starch. Experiments show that this occurs within 2 to 3 weeks after complete defoliation (Parker and Houston 1971, Wargo 1972). It might seem that this is simply a case of starvation, but the situation may be more complex. Mobilization of food reserves similar to that during spring changes may occur. Leaf removal may elicit the translocation of hormones or metabolites in the stems (Kozlowski 1971). When refoliation follows defoliation, root reserves are more sharply depleted than when refoliation does not occur (Wargo et al. 1972). Interruption of stem translocation with and without defoliation should help to clarify the mechanisms that bring about starch hydrolysis in roots of defoliated trees.

This paper reports results of studies in two different years on the effects of several such treatments on starch and sugar levels in sugar maple roots.

METHODS AND MATERIALS

Fifty saplings about 10 m tall and 3 to 6 cm dbh were selected for the 1971 experiment in southern Connecticut. Randomly selected groups of 10 trees were defoliated, girdled, girdled and defoliated, or cut off on June 7. Ten untreated trees served as controls.

Defoliation consisted of bending trees down and plucking off all the leaves, not including petioles, by hand. Girdling was done with a knife at breast height so that a band of bark 3 cm wide was removed all around the tree into the cambium. Cutting off was done by severing the tree 1 m above-ground. After 2 weeks, root systems of half of the trees of each group were excavated and about 30 seg-

ments 10 cm long and 1 cm thick were collected. The remaining trees were harvested after 4 weeks.

The experiment was repeated in 1972 in a different location, again beginning on June 7. This experiment, conducted to confirm the results of 1971, utilized only 25 trees and all were harvested after 4 weeks. The 1971 growing season from mid-June to mid-July was unusually dry compared to 1972, when frequent rains occurred in the same period.

Root samples were brought to the laboratory within 30 minutes and were frozen and stored at -35°C . From the 30 samples per tree, three were taken randomly and two sections were made from each of the three. A freehand cross section, approximately $25\ \mu$ thick was stained with $\text{I}_2\text{-KI}$ for 10 minutes and examined at 100 and 660X (Parker 1970). Three rows of 10 cells each, running tangentially across rays, were examined. The number of cells with starch grains found per row was expressed as a number from 0 to 10. Counts were averaged for the three rows of cells, for the two sections per root, and for the three roots per tree. Since large numbers of specialized starch-containing fiber tracheids occur in sugar maple roots (Parker 1974), it is not unusual to obtain counts of 8 or even 9 in healthy, untreated trees. Because of the variation of scores within each root, counts were classified into four categories: 0 to 1, depleted; 1 to 3, low; 3 to 5, medium; and 5 to 9, high. These four categories correspond closely to those used by Wargo (1974), based on a visual assessment of $\text{I}_2\text{-KI}$ staining without optical aid.

Sugars were determined as follows: From

each seedling 3 segments of root, including bark and wood, totalling 5 g were cut into 3 mm pieces with pruning shears, ground in a Waring blender with 100 ml of 80 per cent ethanol, and filtered under suction through Whatman #1 paper. Other pieces from the same roots were weighed, dried in an oven at 105°C for 24 hours, and reweighed to estimate dry weight. The filter cake was washed with another 50 ml of 80 per cent ethanol and the liquid filtrates combined and evaporated under an air stream to 15 ml. Three 5-lambda drops of the concentrated extract were put on Whatman #1 papers, 23×57 cm, and developed descending in n-butanol, water, and acetic acid 4:5:1. Anisidine and benzidine sprays were used to visualize sugars (Stange 1959, Parker 1962). The density of the visualized sugar spots was compared to that of standards on the same papers using a densitometer with integrator.

Sugar levels were expressed as a percentage of dry weight and are an average of five trees.

RESULTS

Starch

Two weeks after the start of the 1971 experiment, the average root starch of treated trees was slightly lower than that of controls. There were, however, no real differences among treatments, and the data are not presented here.

After 4 weeks in both years, the average root starch of defoliated trees was depleted, whereas that of girdled, girdled and defoliated, or cut-off trees was either low or medium (table 1). There were also differences

Table 1.—Starch and sucrose levels in roots of experimentally treated sugar maples.

Experiment	Controls	Cut off	Girdled	Girdled-defoliated	Defoliated
STARCH					
1971	High	Medium	Low	Low	Depleted
1972	High	Medium	Medium	Low	Depleted
SUCROSE					
1971	0.15	0.12	0.12	0.17	0.09
1972	0.10	0.09	0.11	0.06	0.05

between trees that were cut off and those that were girdled and defoliated (table 1).

Sugars

Sucrose, glucose, and fructose were the only sugars that occurred in sufficient amounts for accurate quantification. Other sugars, when detected, occurred only in trace amounts and are not considered here.

After 4 weeks in both years, there were differences in sucrose among the various treatments (table 1). Trends in sucrose levels correspond rather closely to those of starch. Although an analysis of variance revealed no significant differences among treatments in either year, sucrose was lower in defoliated seedlings than in girdled, cut-off, or girdled and defoliated saplings, just as starch was. Levels of fructose and glucose did not differ appreciably among treatments.

DISCUSSION

Girdling of trees is known to result in some decline in starch in the roots (*Curtis 1935, Woods et al. 1959*). Defoliation, too, as mentioned above, brings about root-starch depletion. The present research shows that total defoliation caused a greater depletion of root starch than girdling.

This might be explained by the fact that carbohydrates can move from the roots up the stem phloem of defoliated trees but are prevented from doing so in trees that have been girdled or severed. Some root starvation (net loss of food reserves) probably resulted from each of the treatments. *Curtis's (1935)*

many experiments with girdling woody plants indicated that most upward carbohydrate movement occurred in the phloem and very little or none in the xylem. However, starch levels in trees that were girdled and defoliated were lower than in those cut off. This difference between two treatments in which the phloem was severed suggests that some upward movement of carbohydrates also occurred in the xylem.

The possibility that a hormone or metabolite produced in the twigs migrates downward to the roots and triggers starch hydrolysis cannot, of course, be proven or disproven by the data. Hydrolysis of starch to glucose can occur as a result of allosteric enzymes that are activated by a small quantity of end product; in this case, glucose (*Lehninger 1971*). The concept of hormone production and transport would not, then, have to be invoked to explain the results of these experiments.

A loss in root starch and sucrose is associated with the spring bud burst (*Wargo 1971*), but it is small compared to that following a June defoliation, which caused a sharp and nearly total loss (*Parker 1970, Wargo 1972*). This difference in response suggests that re-foliating twigs do not produce hormones which, when moved to the roots, cause starch hydrolysis. It is more likely that the twigs have already lost much of their reserves during the spring bud burst; then when a second bud burst occurs as a result of defoliation, a still greater demand is put on food reserves in various parts of the tree, including the roots.

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