REMARKS ON THE PHYSIOLOGICAL EFFECTS OF DEFOLIATION ON SUGAR MAPLE AND SOME IMPACTS ON SYRUP PRODUCTION

Philip M. Wargo

U.S. Department of Agriculture, Forest Service
Northeastern Forest Experiment Station
Center for Biological Control
Hamden, Connecticut USA

The information I am going to present today is a conglomeration of some of the research on the effects of defoliation that has been done on sugar maple and oak. It involves work done by Drs. David Houston, Johnson Parker, Robert Gregory and me. Dr. Houston, a plant pathologist, and Dr. Parker, a plant physiologist, work with the USDA Forest Service in Hamden, Ct.; Dr. Gregory is a plant physiologist who is retired from the Forest Service in Burlington, Vt.

Defoliation

I will describe the effects of defoliation on sugar maple and some of the factors we need to understand about defoliation to anticipate its various effects. For example, defoliation can occur at different times of the year from a variety of causes and have different effects depending on the growing season. Early defoliation (budbreak to late May) can be caused by frost damage or defoliation by thrips. Defoliation can occur mid-season (early June to early July) from the forest tent caterpillar or occasionally the gypsy moth. Late defoliation (mid-July to mid-August) can occur from the saddled prominent caterpillar or leaf skeletonizers. Defoliations after mid- to late August are rare and have little adverse effect on the trees.

Trees can die after defoliation. However, whether a tree lives or dies depends on a number of factors. First, it depends on how severely a tree is defoliated. If the tree is defoliated severely, it usually will refoliate. Refoliation usually results if severe defoliation occurred from early through mid growing season. Defoliations that are severe enough to cause refoliation usually are more deleterious to a tree's health. If the tree does not refoliate, defoliation was not severe enough to cause the old leaf petioles to abscise and trigger the buds formed for next year to refoliate this year; or defoliation was late in the season and the next year's buds already were in the resting stage or dormant stage. Defoliations after mid-August usually do not trigger refoliation.

Another factor is the time of year in which the tree is defoliated. Time of growing season not only controls how trees respond to defoliation but also determines the length of time a tree has to recover. Trees defoliated early in the season have a longer time to recover. In the case of late-season defoliations, growth and carbon storage already has occurred prior to defoliation. Early and late-season defoliations that result in no refoliation usually have the least severe effect on trees. However, late-season defoliations that occur prior to bud dormancy and trigger refoliation can have the greatest adverse effects.

Other factors that determine the consequences of defoliation are health of the tree at the time of defoliation, growing conditions at the time of refoliation, growing conditions after refoliation, and the presence and aggressiveness of secondary organisms (other insects or pathogens that can cause tissue death and eventual tree mortality). These factors determine whether a tree is merely altered physiologically by a defoliation-refoliation episode or whether a tree is adversely affected by the defoliation. Moisture and temperature conditions during the refoliation period control how large the new refoliated leaves will be, while moisture and temperature conditions after refoliation will determine photosynthetic rate and how rapidly a tree will replace carbon lost during the absence of leaves.

The aggressiveness of secondary organisms will determine whether a single defoliation will weaken a tree to become susceptible to the organisms. Health of the tree at the time of defoliation controls the overall response of the tree to defoliation; how rapidly it refoliates and how severely carbon lost during the absence of leaves will affect tissue vitality. Another important factor that determines the consequences of defoliation is the number of successive years of defoliation. Obviously, defoliation for several growing seasons will have a greater adverse effect than a single defoliation. The severity of a defoliation also influences the impact it ultimately has on the tree.

When a tree is defoliated severely it usually refoliates. That occurs usually when about 75% or more of the foliage is removed and the leaf petioles abscise. The buds that were developing for next year open and the leaves formed for next year begin to expand. Sometimes refoliation is prolific as with early defoliations or it can be scattered sparsely as sometimes happens with later defoliations. Defoliations in early August can result in scattered refoliation because some of the buds are already in the resting stage. Latitude affects when trees reach this stage.

Refoliation

Refoliated leaves are only about one-half the size of a normal leaf but are more efficient photosynthetically; they process carbon dioxide faster, though total food production is reduced. A sugar maple leaf is normally about 80-100 cm^2 while refoliated leaves are only 35-40 cm^2. For both normal and the refoliated leaves, size decreases with each successive year of defoliation. In addition to being smaller, refoliated leaves also are fewer in number.

Refoliated leaves usually are out of phase with the growing season depending on when defoliation and refoliation take place. Refoliated leaves are expanding during hotter and drier conditions than occur during normal spring foliation. In autumn, when normal leaves are going through fall coloration, leaves on defoliated-refoliated trees are green and thus are susceptible to the adverse effects of early winter damage from frost or snowstorms. Leaves may be killed quickly, and mineral nutrients and other compounds that normally are captured by the tree during normal autumn senescence before the leaves drop are lost. As a result, the tree may enter the next growing season with deficient amounts of certain minerals.

Defoliated trees may be out of phase with the growing season the following spring. The normal foliation process may be delayed and defoliated trees may lag behind. Leaves on undefoliated trees may be approaching one-half full size while on trees defoliated the previous year, buds are just breaking and the leaves are just unfurling. One week later, leaves on undefoliated trees may be 80-90% expanded, while leaves on defoliated trees are only about half expanded. A defoliated tree is about a week behind in terms of energy capture. While leaves on undefoliated trees are producing enough energy to maintain themselves and new growth, leaves on defoliated trees are still utilizing energy reserves from the stem tissues.

The pattern of foliation the next spring is affected by when defoliation occurred during the previous growing season. Trees may refoliate only from terminal buds. This happens when trees are defoliated early in the season of the previous year. When trees are defoliated in early season, the terminal buds refoliate while the lateral buds formed on the new shoot prior to defoliation abscise. Thus, only the newly formed terminal bud is available for foliation the following spring. Trees defoliated later in the season also refoliate from the terminal buds but the lateral buds that formed on the new shoot prior to defoliation do not abscise. The new terminal buds formed on the refoliated shoot late in the season fail to survive the winter and only the lateral buds are available for spring foliation on the late-defoliated trees. Thus, foliation the next spring on trees defoliated early in the season is dependent on buds formed after defoliation, while on trees defoliated late in the season, foliation depends on buds formed prior to defoliation.

Fate of Buds

The fate of the terminal bud is determined by plastochron duration (the time between formation of pairs of primordia at the apical meristematic dome of the growing tip) and the number of plastochrons after defoliation. These primordia become either scales or leaves. In a normal bud there are about 12 to 16 pairs of primordia formed during a growing season; 8 to 12 pairs form scales and the others form embryonic leaves and undifferentiated primordia. Plastochron duration is short early in the season and increases as the growing season progresses. When a tree is defoliated, the plastochron duration shortens and a defoliated tree can produce primordia faster. An early-defoliated tree that refoliates can form up to 12 new pairs of primordia that become the scales and leaves for next year's bud. However, trees defoliated later in the season, even with a shortened plastochron duration, may only be able to form five pairs of primordia that become scales and leaf primordia. These buds formed late in the season are more susceptible to winter desiccation and winter freeze damage because they have fewer scales to protect the bud. That is why terminal buds formed after early season defoliation usually survive and those formed after late-season defoliation usually die, leaving the lateral buds to form the crown.

When terminal buds and branches dieback, both lateral buds and latent buds at nodes refoliate forming leaf clumps and clusters. These leaf clusters are less efficient photosynthetically, not because individual leaves are less efficient but because the architecture of leaf array is not optimum for capturing sunlight. Because the leaves are clustered close together, there is a greater amount of mutual shading than would have occurred under normal leaf distribution.

Impact on Leaves

Leaves formed the year after defoliation are smaller in size and number. For example, defoliation in June can result in a 35-40% reduction after one year of complete defoliation, 50% after two years, and 60% after three years. Mid-season defoliations usually have a greater impact on leaf size than later or earlier defoliations. The number of leaf clusters also are reduced after defoliation--as much as 60% after three years of defoliation. Thus, a tree that is defoliated severely for three successive years may have much less than 50% of its original leaf area to capture light and CO_2 and manufacture food.

Energy Levels

Defoliated trees have reduced energy levels. Reserve carbohydrates are used when the tree is without leaves, less leaf tissue is available for making new energy, and the growing season is shorter. In autumn, when healthy trees have large amounts of starch stored in ray tissue in stem and root wood, defoliated trees have low or depleted starch depending on how severe the defoliation was and when it occurred. Trees entering the dormant season with low or depleted energy reserves are vulnerable. Sometime between autumn and spring, energy levels may be depleted and tissues may die in both the root and stem.

Energy is important in the response of trees to wounding. The amount of bark and wood involved in the wound response is inversely proportional to the tree's energy level. If the tree is low in energy per unit volume of wood, larger volumes of wood become involved in compartmentalizing wounds. In an energy-deficient tree, the amount of tissue death around a wound and internal discoloration in the wood is much greater than in an energy-sufficient tree.

Defoliation reduces radial growth, the extent of which depends on when defoliation occurs during the season. Late defoliations have less of an impact on growth because the later in the season defoliation occurs, the more radial growth has occurred. Radial growth is reduced proportional to the severity of defoliation and the number of successive defoliations. Since there is a greater amount of dieback around wounds in an energy-deficient tree and there is less closure because that tree is growing slower, wounds put into defoliated sugar maple trees, including tapholes, will be larger and take longer to close.

The effect of defoliation on energy reserves depends on the time of defoliation. Early season defoliation depletes starch initially but the trees have longer to grow after refoliation and there is some recovery. Mid-season defoliation may deplete the starch. Because there is a shorter growing season in which to recover, there is little starch replacement and the effect is greater. Trees defoliated late in the season are not affected nearly as greatly as with earlier defoliation because usually there is no refoliation. However, if refoliation does occur, the effect on energy reserves may be drastic because the remaining growing season is so short.

Sugar Concentrations

Defoliation affects the chemical constituents of the bark and wood. Compared to undefoliated trees, defoliated trees have lower sucrose and higher concentrations of glucose and fructose, especially in the outer wood and cambial zone of the roots. There also is an increase in amino nitrogen compounds in these tissues. These nitrogen compounds give sugar maple syrup its so-called "buddy flavor;" however, there is no research data on the nitrogen content of sap collected for syrup production from defoliated trees.

The sugar concentration of sap in a tree usually increases in autumn as temperatures decrease and freezing temperatures occur. It continues to increase into early winter and then remains relatively constant as freezing temperatures occur continuously. Sap sugar significantly increases in late winter and early spring when alternating freezing and thawing temperatures occur again. Sap-sugar content then decreases as temperatures warm and trees begin to break bud. In experimentally defoliated trees, there were no significant differences in sap-sugar content between defoliated and undefoliated trees at a single point in time. Nor was there a relationship between absolute starch content and sap-sugar concentration. However, in some defoliated sugarbushes or defoliated maple stands, there was a significant reduction in sap-sugar concentration in defoliated trees.

As long as there is some starch in tissues, that starch will be converted to sugar whether it is a defoliated or undefoliated tree. Therefore, at the beginning of the "sugaring season," a defoliated tree may have the same or nearly the same sap-sugar concentration as an undefoliated tree. However, near the end of the season, there may be no more starch in a defoliated tree to convert to sugar and the sap-sugar concentration will decrease. This decrease in sap-sugar content in defoliated trees probably is reflected in the anecdotal information that indicating that the number of gallons of sap needed to make a gallon of syrup is much higher from defoliated sugarbushes: 40 gallons for undefoliated bushes versus 80 gallons for defoliated bushes.

Summary

To summarize, the effects of defoliation are determined by a number of physical, physiological, and environmental factors that interact in a variety of ways and determine how a tree responds to and is affected by defoliation. Because of this, it might be said that no two defoliations are alike.

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Discussion Period

Question: We saw a slide showing heavy defoliation on one side of the road and no defoliation on the other that was controlled. The comment was made that next year the foliage would develop later in the area that was heavily defoliated. Is that because budbreak would be delayed? How would that effect thrips damage?

Answer: It is possible that thrips damage would be less depending on the developmental rate of buds. However, at this time there is no information on the relationship between thrips damage and bud development. No one has followed thrips activity relative to damage from budbreak to complete defoliation. We do know, based on observations and photographs, that leaves are slower to expand on trees that have been severely defoliated than those that were not defoliated. Whether bud break occurs at the same time in defoliated and undefoliated trees I don't know.

Question: Is anybody working on defense mechanisms in trees in relation to thrips damage?

Comment: Not that I know of. However, significant differences in damage levels between trees located side by side have been observed, suggesting that individual trees respond differently to thrips feeding.

This could be a result of a selection process by the thrips or due to differences in bud phenologies among trees. We know that sugar maple trees can differ genetically even though they are closely spatially related.

Question: Do you think that specific features of the tree determine the percentage of defoliation that occurs rather than the number of insects that are colonizing the individual tree?

Comment: I don't know. However, the results reported today show clearly that trees that were completely defoliated by this early season defoliator, ended up with higher starch levels in their roots than those that were only moderately damaged. These results suggest differences in the response of individual trees to insect attack.