PROPOSED SCENARIO FOR DIEBACK AND DECLINE OF ACER SACCHARUM IN NORTHEASTERN U.S.A. AND SOUTHEASTERN CANADA

by

Robert A. Gregory, Mansfield W. Williams Jr, Betty L. Wong and Gary J. Hawley
United States Department of Agriculture, Forest Service, George D. Aiken Laboratory, Burlington, VT 05401, U. S. A.

Summary

A sequence of events is presented that may explain the reported decline of sugar maple trees in the Northeastern United States and Southeastern Canada. The primary factor, caused by defoliation, is a severe reduction in reserve carbohydrates, especially in roots, at the beginning of the leafless period. In this respect, late defoliators - those that defoliate in late July and early August - are much more destructive than those that defoliate in June because it appears that carbon is being utilised in July and August by one or more sinks about as fast as it is being assimilated photosynthetically. This, in conjunction with a loss of foliage for an extended period and limited refoliation, could result in severe carbohydrate depletion. Limited carbohydrate reserves may not be sufficient for normal respiratory activity during the leafless period, or for vernal outgrowth of embryonic shoots. Late defoliation and low carbohydrate reserves also appear to reduce the ability of the trees to acclimate to low winter temperatures; hence, cold winters could result in additional shoot dieback and mortality. Other factors such as drought, atmospheric pollutants, and numerous pathogens may also influence carbohydrate reserves, thus contributing to decline. Key words: Sugar maple, defoliation, starch, sugar, cold tolerance, wood anatomy, radial increment.

Introduction

Occurrences of decline and mortality of sugar maple (Acer saccharum Marsh.) trees in the Northeastern United States and Southeastern Canada have been reported for many years (Giese et al., 1964; Lachance et al., 1983; Tat- tar, 1978). Symptoms of decline are highly visible along roadways and in the urban environment, where the etiology is generally attributed to effects of road salt and moisture stress (Kotheimer, 1967; Lacasse & Rich, 1964; Westing, 1966, 1969). The origins of decline in natural maple stands have been attributed to a number of biotic and abiotic factors (Giese et al., 1964; Lachance et al., 1983; McLaughlin et al., 1985, Vogelmann et al., 1985; Walters, 1964), perhaps due to the general sensitivity of the species to environmental changes (Westing, 1966).

Localised and episodic occurrences of decline have been reported in stands throughout the northern portion of the natural range of sugar maple. Incidents of severe decline and mortality in natural stands in the Lake States (Giese et al., 1964; Walters, 1964), Quebec (Lachance et al., 1983), and Vermont (Kelly, pers. comm.) have been reported following defoliation by the maple webworm (Tetralopha asperatilla Clem.) or the saddled prominent caterpillar (Heterocampa guttivitta Walker). Defoliation by both of these insects occurs late in the growing season (late July, early August), and Giese et al. (1964) suggest that late-season defoliation of sugar maple may be particularly detrimental because succulent refleshed growth is susceptible to early fall frost injury. We also have observed fall frost injury on refleshed tissue, but axillary buds and shoot tissue which were formed prior to defoliation were not injured by frost. We feel that injury to refleshed growth is not sufficient to cause the extensive damage and mortality reported in the literature.

However, late-season defoliation substantially reduces the amount of stored carbohydrates in sugar maple (Gregory & Wargo, 1986). Limited carbohydrate reserves could result in dieback if available energy substrates were insufficient to maintain respiration in living cells throughout the dormant period, or unable to support vernal flower and vegetative shoot development. In addition, carbohydrates are required as an energy substrate for metabolic activity during cold acclimation (Jung & Larson, 1972; Levitt, 1980), and numerous studies have demonstrated that carbohydrate depletion reduces the ability of woody tissue to develop and maintain cold tolerance (Raese et al., 1978; Siminovich, 1981; Siminovich & Briggs, 1953, Yelenosky, 1975).

Defoliation, carbohydrate depletion, reduced cold tolerance, and subsequent winter injury may help explain the localised and episodic...
pattern of maple decline. Because severe late-season defoliation depends on the density of insect populations, a geographically localised pattern of defoliation might be expected. However, heavy defoliation, even in the late growing season, does not always result in decline and mortality. Kelly (pers. comm.) noted severe late-season defoliation in numerous maple stands throughout Vermont in the early 1980's and observed that decline was most severe in northern stands following the unusually cold winter of 1980–81. The episodic nature of maple decline may well result from the synergistic combination of defoliation and low temperature stresses.

Several authors have discussed the possibility that atmospheric deposition of pollutants may promote maple decline (McLaughlin et al., 1985; Vogelmann et al., 1985). While direct phytotoxic effects of atmospheric deposition have not been demonstrated for sugar maple, the introduction of an additional stress agent could exacerbate decline. However, before the impacts of atmospheric deposition can be evaluated, the etiology of maple decline must be understood. The purpose of this paper is to present the results of several preliminary investigations into the origins of maple decline, and to develop a scenario whereby decline might result from the combined influences of late-season defoliation, carbohydrate depletion, restricted cold tolerance, and unusually cold winter conditions.

Materials and Methods

Sugar maple saplings used to study the effects of defoliation on carbohydrate budgets and dormant-season dieback were randomly selected from several hundred 6-year-old saplings growing at the Vermont State Nursery in Essex Junction, VT, U.S.A. Trees were growing at a 1.5 by 1.5-m spacing, were 4–7 cm diameter at the base of the main stem, and about 5 m tall. All trees were vigorous and appeared free from visible symptoms of defect and disease.

In spring of 1984, trees were randomly allocated to one of four defoliation treatments: an undefoliated control, one early growing season defoliation treatment (6 July), and two late-season defoliation treatments (24 July and 3 August). Two late-season defoliation treatments were used because earlier studies (Gregory & Wargo, 1986) had established that late-season defoliations were particularly detrimental to the health of sugar maple. These late-defoliation treatments roughly correspond to expected times of defoliation in natural stands of sugar maple by the saddled prominent caterpillar (Kelly, pers. comm.). The early-season defoliation treatment was used for comparison with late-season treatments to evaluate the effects of defoliation timing on carbohydrate reserves and dormant-season dieback.

At each defoliation date, 16 trees were completely defoliated by excising leaves at the distal end of the petiole. One tree from each defoliation treatment was randomly selected and destructively sampled at 2, 4, 8, 12, 18, 24, and 30 days subsequent to defoliation to evaluate the immediate effect of defoliation on carbohydrate concentrations. An additional tree was sampled on 2 November to assess the effect of defoliation on the carbohydrate concentration of trees entering the dormant period. The extent of refoliation was observed on the eight remaining trees in each treatment and these trees were allowed to overwinter so that the effects of defoliation on dieback and mortality could be measured. Shoot dieback and tree mortality were recorded in June 1985. Dieback was recorded as the proportion of total shoot length that was dead. Trees were considered dead if they exhibited no signs of refoliation in the spring.

An additional 80 trees served as undefoliated controls. Two trees were destructively sampled on each of 40 dates established at weekly intervals from mid-April through July 1984, and biweekly intervals from August through May 1985. Carbohydrate measurements on control trees were used both to evaluate the extent of carbohydrate depletion in defoliated trees and to establish a seasonal pattern of carbohydrate reserves in sugar maple.

Carbohydrates. — The starch and sugar levels for each tree were measured to compare the carbohydrate status of defoliated and control trees on each collection date. Carbohydrate measurements required the destructive sampling of each experimental tree. Samples from each tree included one root segment at least 1 cm diameter and 4–6 cm long from the middle of each of two lateral roots, and one 4-cm-long cross-sectional sample from the main stem at a height of 1 m.

On each sampling date, the bark, phloem, and cambial zone were removed from each root and main stem section. Samples were washed with double-distilled water, dried, and placed in plastic bags over dry ice for transport. At the laboratory, samples were cut into small pieces, freeze-dried, and ground in a Wiley mill to pass a 60-mesh screen. Milled samples were stored at 65°C pending starch and sugar analysis to prevent rehydration.

Concentrations of starch and soluble sugar were determined for all milled xylem tissue samples. For both determinations, 0.010 g of
milled tissue was extracted twice with 5 ml of methanol: chloroform: water (12:5:3 by volume). The combined supernatant was evaporated to dryness and saved for determinations of total soluble sugar. The pellet was hydrolysed with 1 ml of enzyme solution containing 0.010 g amyloglucosidase (Sigma Chemical Co., St. Louis, MO) per 1 ml of 0.1 M acetate buffer at pH 4.5 and assayed by the method of Haisig and Dickson (1979) for starch concentration. The evaporated supernatant was resuspended in 5 ml LC grade water and analysed for total soluble sugars by the dinitrosaliclyc acid assay (Dickson, pers. comm.). The glucose content of starch hydrolysates and the total soluble sugars were determined spectrophotometrically at 450 and 511 nm, respectively, and concentrations were calculated from standard curves.

Cold tolerance. — Laboratory assessments of cold tolerance were used to evaluate the effects of late-season defoliation on the fall cold acclimation of sugar maple trees. Current-year shoots were removed from four randomly selected trees in each of the control and late-defolitated (3 August) treatments on 7 October and 14 November, 1985. On each date, 1.5-cm internode sections were excised and randomly allocated to one of six test temperature treatments. One test temperature treatment was maintained as a nonfrozen control (4°C) while the others were frozen to one of five preselected temperatures at a rate of 3°C per hour. Test temperatures were established at -3, -7, -11, -15, and -19°C for the 7 October trial, and -6, -12, -18, -24, and -30°C for the 14 November trial. Test temperature treatments were allowed to equilibrate at the preselected temperature for 0.5 hour, and then removed and allowed to thaw slowly to 4°C.

Freezing injury to tissue samples was determined by the electrophoretic conductivity method described by Dexter et al. (1932) and Wilner (1960). Critical temperature, defined as the highest temperature at which freezing injury to plant tissues can be determined statistically, was calculated for each replicate of the control and defoliated treatments according to methods described by DeHayes and Williams (1986). Treatment differences in critical temperature were evaluated for each sampling date by one-way analysis of variance.

Wood anatomy. — A separate study was conducted to evaluate the effects of defoliation on secondary xylem anatomy of sugar maple. We sampled twenty-seven 7-year-old trees growing at the Essex Junction nursery that had been defoliated artificially during the 1981 growing season (see Gregory & Wargo, 1986). Three of these trees were defoliated every 10 days beginning 27 May and ending 5 August. An additional three trees served as undefoliated controls.

In the spring of 1983, stem sections containing the 1980 (prededefoliation), 1981 (defoliation), and 1982 (postdefoliation) growth rings were removed from the main stem of each tree at about 1 m above the ground. Transections (10 μm thick) of the three growth rings were stained by the periodic acid-Schiff’s reaction to accentuate starch deposition and cell wall formation. Radial width of the growth rings was measured microscopically with a calibrated ocular micrometer and expressed as a percent of prededefoliation (1980) radial growth for each tree to correct for tree-to-tree variation in radial increment. An angular transformation was used to homogenise variances, and differences in radial growth among defoliation treatments were tested by one-way analysis of variance and treatment means were compared using Duncan’s multiple range test.

Differences in cell growth and development were also evaluated in microtransections. Cell size and the thickness and birefringence of secondary walls were observed in defoliated and control trees.

Results and Discussion

Refoliation. — Although there was some refoliation due to the flushing of developing buds subsequent to each defoliation treatment, the amount declined with progressively later defoliation. The beginning of new shoot development was observed about 2 weeks after defoliation and the leaves were fully expanded in about 1 month.

The number of leaf pairs refoliating after early defoliation (before mid-June) was comparable to the number existing on the subtending shoots prior to defoliation, but the internodes were shorter and the leaves noticeably smaller than on control trees. With progressively later defoliation, fewer of the developing buds foliated, and these were confined increasingly to the more vigorous long shoots. Also, leaves were smaller and often were not fully formed. Refoliation of trees defoliated in late July and early August was confined almost entirely to terminal buds of the most vigorous shoots in the upper crown. These observations were consistent with those reported by Gregory and Wargo (1986).

Autumn carbohydrate concentrations. — We did not observe consistent differences in starch and sugar concentrations between control and defoliated trees within the 30-day periods after the defoliations. By early November, however, starch concentrations in trees of the late-defoliation treatments were noticeably lower.

Downloaded from Brill.com 10/22/2023 01:32:52PM
via free access
than in the control or early-defoliation treatments (Table 1). Sugar concentrations in late-defoliated trees were elevated above those in control or early-defoliated trees, but not to the extent that they would compensate for the low starch concentrations.

The concentration of total carbohydrates in late-defoliated trees was particularly low in roots sampled in early November, an almost exact replication of results from an earlier study (Gregory & Wargo, 1986). Because the roots of sugar maple contain much more living xylem tissue than shoots (Gregory, 1976), much of the reserve carbohydrate is normally found there. Virtually no starch in roots at the beginning of the leafless period could result in serious problems. This seemed to be the case when we observed overwinter dieback and mortality.

**Dieback and mortality.** — The extent of dieback (Table 1) was strongly associated with the extent of starch depletion. There was no dieback in control trees and only a slight amount in early-defoliated trees. However, there was considerable dieback in late-defoliated trees. In fact, two of the eight trees defoliated on 3 August were dead the following spring. These results support the observation of Giese et al. (1964) and Gregory and Wargo (1986) that sugar maple trees are particularly susceptible to overwinter injury and dieback following late-season defoliation.

Giese et al. (1964) attributed dieback, at least partly, to the lack of hardening of refushed postdefoliation shoots and subsequent mortality of this tissue during fall frosts. Gregory and Wargo (1986) also observed this type of injury, but for at least two reasons we believe it is not the primary cause of major shoot dieback: 1) few shoots flushed after late defoliation, leaving the majority of buds and tissue on late-defoliated trees susceptible to frost damage, and 2) even on those shoots that did flush, the pre-defoliation portion of the shoot contained numerous well-developed axillary buds uninjured by fall frost. Overall, only a very small portion of the entire shoot system of late-defoliated trees would be subject to fall frost injury. We feel that a more tenable hypothesis of sugar maple dieback involves insufficient carbohydrate reserves during the leafless period.

**Annual carbohydrate budget.** — We examined the seasonal pattern of carbohydrate concentrations in shoot and root xylem (Figs. 1 & 2) of undefoliated trees to attempt to determine why late-season defoliations might cause low starch concentrations in autumn. Starch and soluble sugars were almost completely depleted in both shoot and root xylem in late May and early June following completion of most new primary shoot growth and leaf enlargement. Concentrations of soluble sugar in shoots remained low throughout the growing season. By contrast, there was a short period of starch accumulation in shoot and root xylem during June followed by a relatively long period, extending into late August, when concentrations remained about the same. Then, in a 2-week period in early September, xylem starch concentrations nearly doubled, reaching an annual high in mid-September. These relatively high concentrations persisted until the onset of starch dissolution in autumn, induced, presumably, by low temperatures (Marvin et al., 1971; Nelson & Dickson, 1981; Sauter, 1967; Siminovich & Briggs, 1954). Gradual resynthesis of starch occurred with the advent of warmer weather in late winter and early spring, followed by a rapid dissolution and consumption coinciding with vernal metabolic activity. The pattern in sugar maple xylem noted in this study is, in many respects, similar to that reported for this and other woody deciduous species (Gregory & Wargo, 1986; Jones & Bradlee, 1933; Sauter, 1966; Siminovich et al., 1953).

---

Table 1. Early-November starch and sugar concentrations (mg g⁻¹) and associated overwintering shoot dieback for control and defoliated trees.

<table>
<thead>
<tr>
<th>Defoliation date</th>
<th>Starch concentration</th>
<th>Sugar concentration</th>
<th>% Dieback</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>shoot</td>
<td>root</td>
<td>shoot</td>
</tr>
<tr>
<td>Control</td>
<td>7</td>
<td>39.0</td>
<td>0.3</td>
</tr>
<tr>
<td>6 June</td>
<td>7</td>
<td>30.0</td>
<td>0.0</td>
</tr>
<tr>
<td>24 July</td>
<td>5</td>
<td>3.0</td>
<td>1.0</td>
</tr>
<tr>
<td>3 August</td>
<td>2</td>
<td>0.8</td>
<td>1.0</td>
</tr>
</tbody>
</table>
Fig. 1. Seasonal variation in starch concentration of the secondary xylem in sugar maple roots and shoots.

Fig. 2. Seasonal variation in concentration of total soluble sugar in the secondary xylem of sugar maple roots and shoots.
The stable period of starch concentration during July and August suggests that a metabolic sink or combination of sinks existed and utilised carbon about as fast as it was being assimilated photosynthetically. Previous studies (unpublished) indicated that annual production of secondary xylem in sugar maple shoots was about 80 percent complete by mid-July. In lateral roots, however, Wargo (1979) observed that wood production began in early July and continued through August. There is also the possibility that primary (fine) root production may occur simultaneously. Whatever the sink(s), assuming that they do exist, the loss of all leaves for 2 to 4 weeks during this period, combined with the added drain of defoliation, could greatly reduce carbohydrate supply. In addition, the amount of defoliation after late defoliation is noticeably less than in control and early-defoliated trees, adding to the likelihood that recovery after defoliation would be limited. Because the concentration of starch in the xylem appears to double during the brief period from early to mid-September (Fig. 1), any factor that might cause premature decline in photosynthesis—such as drought or photochemical oxidants—might reduce appreciably the level of carbohydrates in storage tissues at the beginning of the leafless period.

Total soluble sugars (Fig. 2) reached their highest annual concentrations during early winter and then declined sharply in shoots in January and February with the onset of colder winter temperatures. A similar winter decline in sap sugar was noted in an earlier study (Gregory & Wargo, 1986). We do not know if there was a corresponding drop in roots at this time because root samples were not collected due to frozen soil.

The cause of decline in the concentration of xylem sugars in shoot xylem in winter is unknown, but the loss did coincide with an extended period of low temperature when daily maxima were consistently below freezing and minima were -15°C or less. These low temperatures may have induced the conversion of soluble sugars into fats as reported by Ziegler (1964). Because an increase in lipid concentration, particularly phospholipids, has been associated with the development of cold tolerance (Clarkson et al., 1980; Graham & Patterson, 1982; Sikorska & Kacperska-Palacz, 1979; Siminovitch et al., 1968), a restricted energy substrate might well limit the ability of late-defoliated trees to fully acclimate to low winter temperatures. This limitation may predispose late-defoliated trees to winter injury, particularly during periods of unusually low winter temperature.

Cold tolerance. — The cold tolerances of trees in the control and late-defoliated treatments were similar on the 7 October sampling date, with mean critical temperatures of -10.3 and -8.2°C, respectively (Table 2). Minimum daily temperatures in the nursery before this date were consistently above 4°C. However, subsequent to the October sampling date, minimum temperatures were often below freezing. Following the onset of cold weather, trees in the control treatment acclimated rapidly, and by 14 November the mean critical temperature of trees in this treatment had decreased to -25.5°C (Table 2). These results are consistent with reports of rapid cold acclimation in other hardwood species following the onset of cold temperature in the fall (Flint, 1972; Smithberg & Weiser, 1968; Williams, 1984). The cold tolerance of trees in the late-defoliation treatment also increased substantially from October to November, reaching a mean critical temperature of -19.6°C by 14 November (Table 2). However, cold tolerance in these trees was significantly less (P < 0.05) than in control trees, a difference of nearly 6 degrees. Thus, it appears that late season defoliation substantially impedes the process of fall cold acclimation in sugar maple. Because carbohydrate reserves, particularly root starch concentrations, were considerably lower in late-defoliated trees (Table 1), perhaps the energy substrates in these trees were insufficient to support the metabolically active process of cold acclimation.

Table 2. Mean critical temperature in control and late-defoliated trees in October and November 1985.

<table>
<thead>
<tr>
<th>Collection date</th>
<th>Mean critical temperature (°C)</th>
<th>Probability of &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Defoliated</td>
</tr>
<tr>
<td>7 October</td>
<td>-10.3</td>
<td>-8.2</td>
</tr>
<tr>
<td>14 November</td>
<td>-25.5</td>
<td>-19.6</td>
</tr>
</tbody>
</table>
Table 3. Radial growth of control and defoliated trees as a function of date of defoliation. Mean radial growth in the year of defoliation (1981) and the year after defoliation (1982) is expressed as a percentage of radial growth the year before defoliation (1980). Radial growth in 1981 that occurred after defoliation is expressed as a percentage of total 1981 radial growth.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1981</td>
<td>1982</td>
</tr>
<tr>
<td>% of 1980 growth</td>
<td>% of 1981 growth</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>115 a*</td>
<td>117 a</td>
</tr>
<tr>
<td>5 August</td>
<td>91 a</td>
<td>19 b</td>
</tr>
<tr>
<td>26 July</td>
<td>66 bc</td>
<td>35 b</td>
</tr>
<tr>
<td>16 July</td>
<td>77 bc</td>
<td>21 b</td>
</tr>
<tr>
<td>6 July</td>
<td>60 bc</td>
<td>42 b</td>
</tr>
<tr>
<td>26 June</td>
<td>43 cde</td>
<td>54 ab</td>
</tr>
<tr>
<td>16 June</td>
<td>47 cd</td>
<td>53 ab</td>
</tr>
<tr>
<td>6 June</td>
<td>20 e</td>
<td>48 ab</td>
</tr>
<tr>
<td>27 May</td>
<td>24 de</td>
<td>63 ab</td>
</tr>
</tbody>
</table>

* Percentages within each year (column) with the same letter are not significantly different, Duncan (P < 0.05). For example, there was no significant difference in radial growth in 1981 between control and 5 August defoliated trees, but radial growth of those trees was significantly different from trees defoliated at other times in 1981.

Wood anatomy. – There were noticeable differences in the overall production and degree of differentiation of secondary xylem cells as a result of defoliation. The degree and extent of these differences were related to time of defoliation. In all cases there was a reduction in radial width of the annual rings (Table 3), a reduction in secondary wall formation of axial elements that were differentiating at the time of defoliation (Figs. 4–7), and a decrease in the radial width of axial elements produced shortly before and after defoliation (Figs. 7 & 8).

Under low magnification, when the entire radial width of the 1981 growth ring is in view, one can observe in transections a tangential band of radially narrow nonlatewood cells in defoliated trees that was obviously related to defoliation (Fig. 7). We considered that the outer axial elements of these bands closely approximated the position of the inner margin of the cambial zone at the time of defoliation, and that xylem tissue inside and outside that position was produced before and after defoliation respectively. This assumption, and hence the precision of our measurements, may be slightly flawed because we do not know exactly how defoliation affects cambial activity; whether cambial activity ceased and then resumed or only slowed down. These radially narrow cells may have been produced prior to, during, or just after defoliation, or a combination of all three. In any case the measurement error would be slight since the radial width of this zone is narrow relative to that of the entire annual ring.

Defolations early in the 1981 growing season reduced that year's wood production more than later defoliations (Table 3 column 2). There was some detectable wood production after the earliest defoliations (27 May and 6 June), but very little in trees defoliated later (Figs. 7, 10; Table 3 column 4). However, in the next growing season (1982), trees defoliated late in the previous year did not produce as much wood as trees defoliated earlier that year (Table 3 column 3).

The magnitude of birefringence, which reflects alterations in the orientation and quantity of microfibrils in cell walls, was appreciably less in axial elements that were differentiating at the time of defoliation (Figs. 3–6, 7, 8, 11, 12). Birefringence in axial elements produced...
before and after defoliation appeared similar to that in axial elements of control trees (Figs. 7, 8, 11, 12, 13, 14). Secondary wall thickness in defoliated trees was much less than in controls (Figs. 3–6), hence the reduced birefringence.

It also appeared that cells produced just before and after defoliation, in addition to being less birefringent, did not enlarge radially, thus sometimes creating the appearance of latewood (Figs. 7, 10). However, they differed from normal latewood (Fig. 9) in two respects: they had relatively thin secondary walls, and there were no radial files of axial parenchyma as in terminal wood (Figs. 7, 10). The parenchyma files in the true terminal wood of defoliated trees (Fig. 10) were usually less orderly than those in control trees (Fig. 9).

It appears that we might be able to identify previous defoliation in natural stands on the basis of a combination of wood characteristics including a reduction in (1) annual radial growth, (2) cell wall thickness, (3) birefringence of secondary walls, and (4) radial width of axial elements. Because of the abrupt nature of the defoliation-induced stress, one would expect these reductions to be more sharply defined than other environmentally induced stresses such as drought. We might also be able to distinguish whether defoliations were caused by an early defoliator such as the forest tent caterpillar (Malacosoma disstria Hbn.) or a late defoliator such as the saddled prominent caterpillar. We are presently examining wood characteristics in natural stands for which records of insect defoliation exist to determine if this is indeed feasible. If so, one might be able to establish periods of past maple decline and changes in stand structure resulting from such declines.

Other possible stresses: Throughout the natural range of sugar maple it is common to have little or no precipitation for several successive weeks during the growing season. Drought alone, or in combination with other stresses, could be a factor in sugar maple decline. We are currently studying the effects of drought alone and in combination with defoliation, on the quantities of stored carbohydrates, cold acclimation, and overwinter dieback and mortality in sugar maple trees.

Recent studies have shown that ambient levels of ozone cause growth reductions of some deciduous tree species including seedlings of sugar maple (Reich et al., 1986; Wang et al., 1985). Thus ozone might be a factor in sugar maple decline, especially in concert with natural biotic and abiotic stresses. Since ozone is reported to limit photosynthesis and cause premature leaf senescence, it may be detrimental, especially in combination with defoliation, by reducing concentrations of stored carbohydrates.

Establishing a tenable cause and effect scenario for decline in natural ecosystems will most

(text continued on page 368)

Legends to Figures 3–14:

Fig. 3–6. Transctions of stemwood from control and defoliated trees; all x 500. – 3 & 4: Control tree: normal secondary wall formation, bright field (3) and same field showing normal birefringence, crossed polarisers (4). – 5 & 6: Defoliated tree: elements that were differentiating at the time of defoliation illustrating relatively thin secondary walls (5) and, in same section, reduced birefringence (6).

Fig. 7–10. Transctions of stemwood from control and defoliated trees; 7 & 8 x 144; 9 & 10 x 312. – 7: Tree defoliated 27 May shortly after the beginning of annual xylem production: thin-walled, radially enlarged (RE) and radially narrow (RN) cells that were differentiating at the time of defoliation. – 8: Same section as Fig. 7 showing reduced birefringence in elements that were differentiating at the time of defoliation. – 9: Control tree: normal latewood with tangentially aligned terminal parenchyma. – 10: Tree defoliated 16 June: thin-walled, radially enlarged (RE) and radially narrow (RN) elements that were differentiating at the time of defoliation; terminal parenchyma cells were probably produced after defoliation.

Fig. 11–14. Transctions of stemwood of defoliated and control trees; all x 140. – 11: Tree defoliated 5 August toward the end of annual xylem production: thin-walled, radially enlarged (RE) and radially narrow (RN) cells that were differentiating at the time of defoliation are confined to end of growth ring; terminal parenchyma present but tangentially irregular. – 12: Same section as Fig. 11 showing reduced birefringence in elements that were differentiating at the time of defoliation. – 13 & 14: Control tree: normal development (13) and birefringence (14).
likely involve an understanding of the physiological and developmental responses of trees not only to individual stresses, but to combinations of stresses. The methods employed for studying the effects of atmospheric deposition on forest ecosystems most often evolve from those used with agricultural crops where natural factors such as insects, disease, and drought can be controlled with insecticides, fungicides, or by irrigation. In natural forests, however, it is seldom practical to control such factors and it is common for trees to be stressed by one or more of them at any given time. In addition, trees are perennial plants, and they must store considerable substrate for maintenance respiration, cold acclimation and vernal outgrowth of flower and vegetative shoots. Hence, one should consider additional variables common to forest ecosystems that are not normally factored into conventional dose-response experiments on the effects of atmospheric deposition in order to realistically evaluate their synergistic and antagonistic effects.

Acknowledgements

We thank Ronald Kelly, insect and disease specialist, Vermont Department of Forests, Parks and Recreation for sharing information on the incidence and severity of insect defoliation in Vermont and Richard E. Dickson, Forestry Sciences Laboratory, Rhinelander, Wisconsin for advice in determining soluble sugar concentrations in xylem tissues. We are also grateful for the technical help of Kelly Baggett and John Bennink of our laboratory.

References


