

Studies of Maple Blight

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Part I. A New Condition of Sugar Maple

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Studies of MAPLE BLIGHT

PART I.

A New Condition of Sugar Maple¹

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Introduction

THE UPLAND NORTHERN HARDWOODS represent a forest type of great economic, biotic and aesthetic value throughout northeastern and northcentral United States and in southeastern Canada. Sugar maple, *Acer saccharum* Marsh., is usually the leading dominant in these stands in terms of numbers of trees and in size. Often the economy of the areas depends largely on the lumber produced

from maple. For instance, in 1954, over 54,000,000 board feet of maple were cut from 2,663,000 acres of northern hardwoods in Wisconsin alone (Horn, 1957; Stone and Thorne, 1961).

In recent years, a slow decline in vigor and frequent mortality of mature sugar maples occurred in northeastern United States and in southeastern Canada. The condition has been referred to as maple

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dieback. In 1957, foresters of the Goodman Division of Calumet and Hecla, Incorporated, reported a new condition characterized by the sudden deterioration of the crowns and the death of thousands of sugar maple trees and saplings in mixed northern hardwood stands (Fig. 1). This condition occurred in areas of various sizes scattered over 10,000 acres in Florence County in northeastern Wisconsin. The disease occurred in stands with a history of intensive management and selective logging that in the previous several years had sustained severe defoliation by a complex of insects. Because of the rapid deterioration of all age class trees, the condition came to be known as *Maple Blight*.

Characterization of Maple Blight

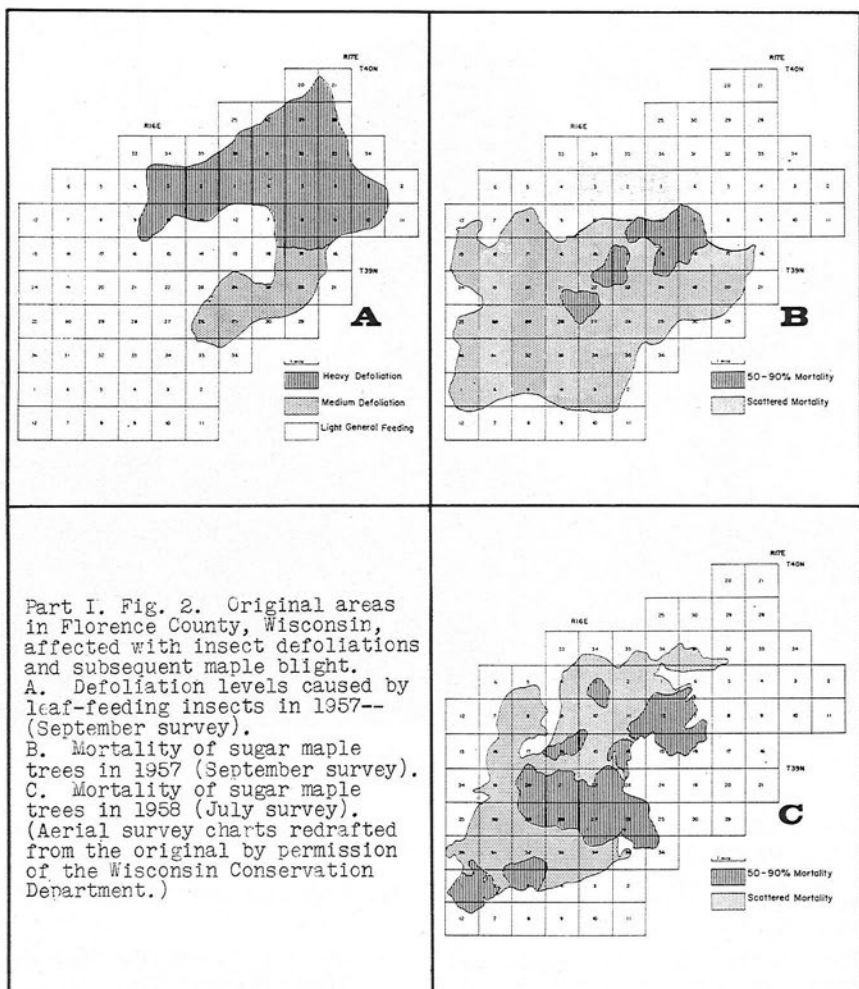
Perhaps the most striking gross characteristic of maple blight was the pattern of distribution. Though trees on about 1000 acres died, the affected areas did not represent a continuous stand of trees. Severe mortality occurred in small localized pockets (Fig. 2B, C).

From 4 years of observations, a qualitative characterization can be made; symptomatology probably represents a successional system. The 4 stages usually manifested in blighted areas may all exist or the condition may progress to any of the following levels:

- 1) *Branch Dieback*, one of the earliest symptoms is a condition in which the mortality of the terminal por-



Part I, Fig. 1. Mortality of sugar maple growing stock resulting from maple blight.



tions of branches imparts an appearance of marginal thinness to the crown of the tree.

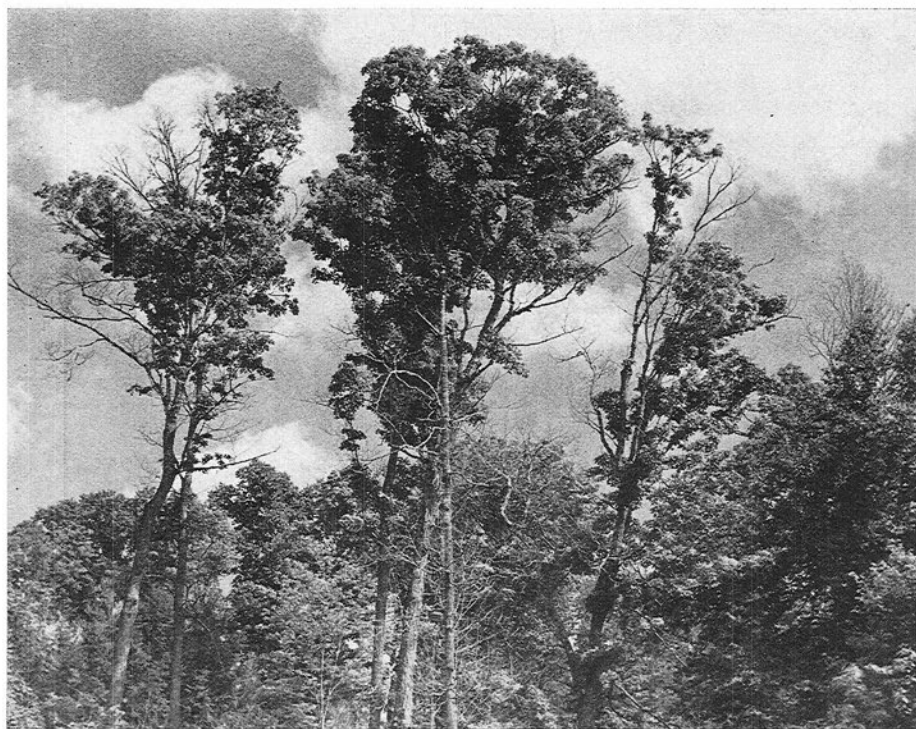
- 2) *Foliage Chlorosis* and *Wilt* are followed by brown or red coloration and finally death during the growing season. The next year, foliage is small.
- 3) *Epicormic Sprouting* is the elaboration of great numbers of dormant buds (Fig. 3) at sites other than the axils of leaves or apices of stems. Normal leaf buds give rise to small, sparse, yellowed foliage.
- 4) *Tree Mortality* is the final stage of this abnormal physiological con-

dition (Fig. 1). Death of the trees (as well as decline of vigor) may occur in all age and dominance classes.

Deterioration of the trees is usually rapid and may proceed up from the base or down from the top or may be exhibited in a random branch-by-branch decline. Symptomatology of the disease is described in more detail in Part III.

Objectives of the Investigation

Maple blight represented the first recorded instance of a biotic catastrophe in the climax upland northern hardwood



Part I, Fig. 3. Epicormic sprouting elaborated by sugar maple in a maple blight area.

forests of the Lake States. This was of particular significance as it occurred in a forest being managed silviculturally by approved practices. The potential threat of this disease to extensive stands of northern hardwoods in Wisconsin and adjacent Lake States prompted the immediate attention of several cooperating research agencies.

In 1958, a cooperative research and survey program was initiated to investigate maple blight. The Departments of Entomology and Plant Pathology of the University of Wisconsin, the Wisconsin Conservation Department and the Lake States Forest Experiment Station of the U.S. Forest Service cooperated to investigate entomological, pathological, distributional and ecological factors associated with maple blight. The reports of these coordinated investigations of maple blight are presented in the following 5 parts:

I. Maple Blight—A New Condition of Sugar Maple.

II. The Insect Complex Associated with Maple Blight

III. Pathogens Associated with Maple Blight.

IV. Defoliation and the Genesis of Maple Blight

V. Ecological Factors Associated with Maple Blight.

Ecological Description of Affected Forests

FLORENCE COUNTY LIES within the Northern Highland geographical province. The immediately underlying rock is pre-Cambrian in origin and the range in elevation is from 1250-1500 feet (Martin, 1916). The soil supporting the forest is a gray-brown podzolic type (Curtis, 1956).

The general area is included in the northern conifer-hardwood province of Curtis (1959) and is characterized by low

temperatures and a short growing season (Wang and Suomi, 1957). The normal dates for the last killing frost in the spring and the first in the fall are May 20 and September 16, respectively. The normal growing season (above 32° F.) is 118 days; however, the native season (above 28° F.) normally affords 151 days of growth. The season of growth for cultivated plants lasts 50-80 days; this contrasts greatly with the longest (140 days) growing season in Wisconsin. The blighted stands are encompassed by a zone of advection frost during the growing season.

The normal daily temperatures, averaged monthly, for Florence County range from west to east as follows: January, 10-14° F.; May, 50-54° F.; July, 64-68° F.; October, 44-46° F. Maple blight occurred in an area adjacent to an isothermic island that represents the lowest July temperature in the state (Wang and Suomi, 1958). The mean summer temperature is 65° F. (Curtis, 1956). The area usually receives about 55 inches of snowfall annually. Based on 37 years of records (Coleman, 1941), Florence County has a mean annual precipitation of 30.45 inches.

The northern hardwood type in Wisconsin is an all-age and all-size structure dominated by sugar maple in association with hemlock, *Tsuga canadensis* (L.) Carr.; yellow birch, *Betula alleghaniensis* Britton and basswood, *Tilia americana* L. The lower strata of the maple stands are

sparsely populated with shrubs and herbs, except in the early season when the spring ephemerals carpet the forest floor. The canopy is dense and frequently less than 100 footcandles of light are available to plants close to the soil surface, as contrasted with about 10,000 footcandles for plants in full sunlight. Seedling and sapling growth is limited to shade tolerant species, such as sugar maple and those that can propagate vegetatively, such as hemlock and basswood.

This northern forest type exhibits a high degree of compositional stability (Curtis, 1959); it is a terminal or climax forest. Sugar maple, the greatest potential dominant, replaces hemlock, another shade tolerant competitor. Yellow birch, basswood, elm, *Ulmus americana* L. and ash, *Fraxinus americana* L., the other major trees in the type, persist only in the gaps or openings resulting from lightning strikes and windthrows (Curtis, 1959).

Seed production exceeded 8,000,000 seeds per acre in one virgin stand and 4,000,000 per acre in a selectively logged stand (Godman, 1957). Commonly, less than 50% of the seeds are viable and less than 50% of the first year seedlings survive (Curtis, 1959). The great seed production and the capacity to subsist under conditions of intense competition for light, moisture and nutrients set sugar maple high on the scale of vitality (degree of success in the community) and adapt it well for dominant behavior.

Materials and Methods

The Relationship of Forest Stand Characteristics to Maple Blight

Preliminary examination of the hardwood stands afflicted with maple blight suggested strongly that stand structure and species composition might have a gross effect on the development of the condition. To obtain a more exact quantitative impression of the severity of maple blight in different stands within the more generalized affected area, and to compare stand characteristics within the blight area to those outside, 7 stands in and

7 stands adjacent to the primary blight area were sampled (Table 1). This enabled the comparison of stands over a geographical gradient, yet over a similar physiognomical area.

The stands were sampled by means of the point sampling system known as the quarter method (Cottam and Curtis, 1956), which prescribes that the nearest tree or sapling in each of 4 quarters at 40 predetermined points will be measured with respect to distance, species and diameter. (Saplings are defined as stems 1 to 4 inches in diameter; trees as stems over

Part I, Table 1. Locations and ownerships of mixed northern hardwood stands evaluated in maple blight study.

Stand No.	Township (North)	Range (East)	Section	General location	Ownership
1	38	16	2	South Goodman Grade	Goodman Lumber
2 ¹	39	16	26	Camp Sheboygan	Goodman Lumber
3 ¹	39	17	7	Patten Lake Spur	Goodman Lumber
4 ¹	39	16	26	Branch Line 2	Goodman Lumber
5 ¹	39	17	20	HY 101 and Patten Lk. Rd.	Goodman Lumber
6 ¹	39	16	21	Volkler's Spur	Goodman Lumber
7 ¹	39	16	11	N.W. Consolidated Comp.	Goodman Lumber
8 ¹	39	16	23	Vassar	Goodman Lumber
9	36	17	21	South of Goodman	Goodman Lumber
10	38	15	32	East of HY 139	Connor Lumber
11	36	14	29	West of Laona, HY 8	Connor Lumber
12	40	16	28	East of Silv. Doll. Lk. HY 70	U.S. For. Ser.
13	40	16	29	West of Silv. Doll. Lk. HY 70	U.S. For. Ser.
14	38	17	34	East of Fence	State of Wisconsin

¹ Stands in which maple blight occurred.

4 inches.) The method was modified in the diseased stands to accommodate two complete sets of data. In the first measurement, the closest trees and saplings (dead or alive) present prior to the maple blight attack were recorded. Stems which had been salvaged because of maple blight were distinguished from those of the economic harvest by an identifying red mark placed below the cut in addition to or in place of the regular blue cutting code or axe blaze. The second measurement involved the recording of living trees and saplings only. Frequencies, densities and dominances were calculated according to standard procedures of Curtis (1956).

Each stand was characterized with a vegetational continuum index (Brown and Curtis, 1952) which allows between-stand comparisons. Tree species for which no adaptation number was available (*Ulmus thomasi* Sarg.) were assigned an arbitrary value of 5. Although this value may not be accurate, the importance of these trees is low and little error is introduced. For saplings, the importance value (I.V.) = relative density + relative frequency $\times 1.5$. The I.V. calculated by

this technique cannot be construed as having had the correct dominance inserted; rather, it allows a placement on the same 0-300 basis as the real importance scale, and permits a direct numerical, but not necessarily actual, comparison with that of the trees.

The concept of relative importance (R.I.) is introduced here to enable an expression of species comparative prominence: $R.I. = \frac{\text{Importance Value}}{3}$. Thus

the R.I. value of a species is directly comparable with other species on an understandable 1-100 (percentage) scale. Such an index, utilizes a combination of density, dominance and frequency (when available) and presents a more complete image of species placement in a stand than a single factor because the influences of spatial, numerical and volume distribution are all considered.

Stands are named for the species of greatest magnitude in continuum index values. These values reflect the current status of the stand in terms of size, numbers and distribution, and to some degree, to its potential as well.

Results

Characterization of Non-Blighted Mixed Northern Hardwood Stands Adjacent to Area Afflicted with Maple Blight⁶

Seven mixed hardwood stands adjacent to blighted areas were studied in Florence County. Nineteen tree species were present in these stands (Table 2). These stands averaged 2624 and ranged from 2420 to 2734 along the continuum gradient for trees (Table 3).

Sugar maple was the leading dominant tree species with a mean relative importance value of 44.4% (Table 3). Hemlock, American elm, yellow birch and basswood were the next leading dominant species with mean relative importance values of 21.5, 10.6, 7.6 and 5.8% respectively. Sugar maple constituted 91 of

the average 177 total trees per acre or 51.4%.

The relative importance values of the sapling sugar maples were higher than those for the trees, due primarily to the increased percentage of sugar maple in the sapling layer. Otherwise, the species composition and relative importance values of the sapling layer were usually about the same as for the tree layer.

Characterization of Blighted Mixed Northern Hardwood Stands Prior to the Occurrence of Maple Blight

The 7 mixed hardwood stands evaluated in the blighted area averaged 2671 and ranged from 2607 to 2733 along the continuum gradient prior to the development of the disease (Table 4). Sugar maple

⁶ Information relative to the statistical procedure and data employed in the calculation of Relative Importance and Continuum Indices for this investigation is available at the Wisconsin Agricultural Experiment Station, Madison, on request.

Part I, Table 2. Tree species encountered and their presence in maple blight study stands.

Species	Common name	Number of stands (of possible 14) in which species occurred as	
		Saplings	Trees
<i>Abies balsamea</i> (L.) Mill.	balsam fir	2	7
<i>Acer rubrum</i> L.	red maple	2	2
<i>Acer saccharum</i> Marsh.	sugar or hard maple	14	14
<i>Acer spicatum</i> Lam.	mountain maple	5	0
<i>Betula alleghaniensis</i> Britton	yellow birch	14	14
<i>Betula papyrifera</i> Marsh.	white or paper birch	0	2
<i>Fraxinus americana</i> L.	white ash	2	3
<i>Juglans cinerea</i> L.	butternut	0	2
<i>Ostrya virginiana</i> (Mill.) K. Koch	ironwood	14	14
<i>Picea glauca</i> (Moench) Voss	white spruce	1	2
<i>Populus grandidentata</i> Michx.	big tooth aspen	1	2
<i>Prunus pensylvanica</i> L.f.	pin cherry	1	0
<i>Prunus serotina</i> Ehrh.	black cherry	4	4
<i>Quercus rubra</i> L.	northern red oak	0	1
<i>Thuja occidentalis</i> L.	northern white cedar	0	2
<i>Tilia americana</i> L.	basswood	13	14
<i>Tsuga canadensis</i> (L.) Carr.	eastern hemlock	4	13
<i>Ulmus americana</i> L.	american elm	13	14
<i>Ulmus thomasii</i> Sarg.	rock or cork elm	3	2

Part I, Table 3. Characterization of seven non-blighted mixed northern hardwood stands adjacent to blighted areas in Florence County.

Stand no.	Relative importance value of tree species						Relative importance sugar maple saplings	Trees per acre		Continuum index trees
	Sugar maple	Hemlock	Yellow birch	Basswood	American elm	Others		All trees	Sugar maple	
13	56.3	8.3	4.9	7.5	18.2	4.8	38.2	156	92	2,734
9	48.5	14.4	21.4	2.7	6.2	6.8	61.3	204	106	2,702
1	47.9	28.1	8.2	2.2	6.8	6.8	59.8	171	88	2,697
10	47.0	20.1	4.4	5.8	19.1	3.6	54.6	157	83	2,693
11	37.4	44.6	5.5	3.9	5.0	3.6	61.0	117	51	2,610
12	30.3	35.3	4.9	5.8	12.2	11.5	78.9	208	115	2,512
14	43.2	0.0	3.6	12.8	6.5	33.9	68.9	224	99	2,420
Total	310.6	150.8	52.9	40.7	74.0	71.0	422.7	1237	634	18,368
Mean	44.4	21.5	7.6	5.8	10.6	10.1	60.4	177	91	2,624

Part I, Table 4. Characterization of mixed northern hardwood stands
prior to the development of maple blight.

Stand no.	Relative importance value of tree species						Relative importance sugar maple saplings	Trees per acre		Continuum index trees
	Sugar maple	Hemlock	Yellow birch	Basswood	American elm	Others		All trees	Sugar maple	
7	50.7	14.4	9.3	5.9	5.6	14.1	83.2	147	79	2,733
6	52.3	14.6	12.4	4.0	6.3	10.4	71.2	145	82	2,728
8	38.9	22.8	16.6	3.1	12.4	6.2	91.6	153	67	2,644
4	49.4	18.5	10.6	3.5	8.5	9.5	65.0	159	85	2,705
2	46.5	15.2	9.7	7.9	14.8	5.9	64.4	177	92	2,664
3	34.7	26.1	14.1	3.7	10.5	10.9	79.8	150	63	2,607
5	34.5	23.2	18.9	7.4	6.2	9.8	38.9	221	68	2,613
Total	307.0	134.8	91.6	35.5	64.3	66.8	494.1	1152	536	18,694
Mean	43.8	19.3	13.1	5.1	9.2	9.5	70.6	165	76	2,671

was the leading dominant with a mean relative importance value of 43.8%. It constituted 46.1% of the total trees per acre. Hemlock, yellow birch, American elm and basswood followed with mean relative importance values of 19.3, 13.1, 9.2 and 5.1% respectively. Again the relative importance values of sugar maple saplings reflected the increased percentages of this species in the sapling layer.

On the basis of relative importance value of trees and the other factors cited in Tables 3 and 4, the non-blighted northern hardwood stands adjacent to the blighted area appear similar to those in which blight later occurred.

Characterization of Mixed Northern Hardwoods Following the Occurrence of Maple Blight

Following the occurrence of maple blight the seven mixed northern hardwood stands showed a slightly reduced mean continuum index value of 2636 and a range from 2610 to 2708 (Table 5). Sugar maple continued to be the leading dominant, but its mean relative importance value declined to 38.1%. Hemlock, yellow birch, American elm and basswood continued to be the next leading dominant species with relative importance values of 21.8, 13.4, 10.2 and 5.4% respectively. The mean relative importance of the sapling layer declined slightly to 64.4%. Sugar maple constituted 53 of the mean 133 trees per acre or 39.9%.

In the diseased stands, mortality among the sugar maple trees averaged 15.2% and among the saplings 33.0% (Table 6). The distribution of the tree mortality declined curvilinearly from the smallest to the largest size class and reflects the skewness toward the small end of the diameter scale. The greatest number of trees generally will be found in the smallest diameter classes in this type hardwood community (Table 7). In a practical sense, the growing stock was depleted; over 90% of the trees that died were less than 11 inches in diameter.

Intra-class mortality is reflected in a different manner and demonstrates a parabolic curvilinear relationship where the

smallest and largest trees exhibit greatest susceptibility (Fig. 4). Intermediate sizes (usually vigorous) show less effect if measured by mortality, if one assumes a nearly uniform time and space distribution of a causal agent. Such a pattern suggests that suppressed and overmature maples were affected to a greater extent than were intermediate trees.

Mortality did not affect the spatial pattern of sugar maple as evidenced by the absolute frequencies of saplings and trees that were only slightly or not at all reduced. The relative importance of sugar maple was reduced an average of 5.7% following blight, and in the case of the stands 3 and 7, this reduction was 8.7 and 15.9% respectively.

Stand 3 was intensively studied (by a 100% sample of 4.2 acres taken in 0.1 acre units in 1960-61) because it was one of the most severely affected of those examined. In this stand there was a reduction of 46.2% in the basal area of sugar maple trees. The loss in tree numbers was even more drastic (Table 8): a reduction from 68 to 32 maple trees per acre (53%) and a 30% loss of all tree species numbers leaving a residue of 85 trees (all species) per acre. Of a pre-blight 385 maple saplings per acre, 49.5% died, leaving 195 sugar maple saplings. Considering all species of this small size class, the mortality of maple saplings resulted in a 46.6% reduction in all species sapling stand.

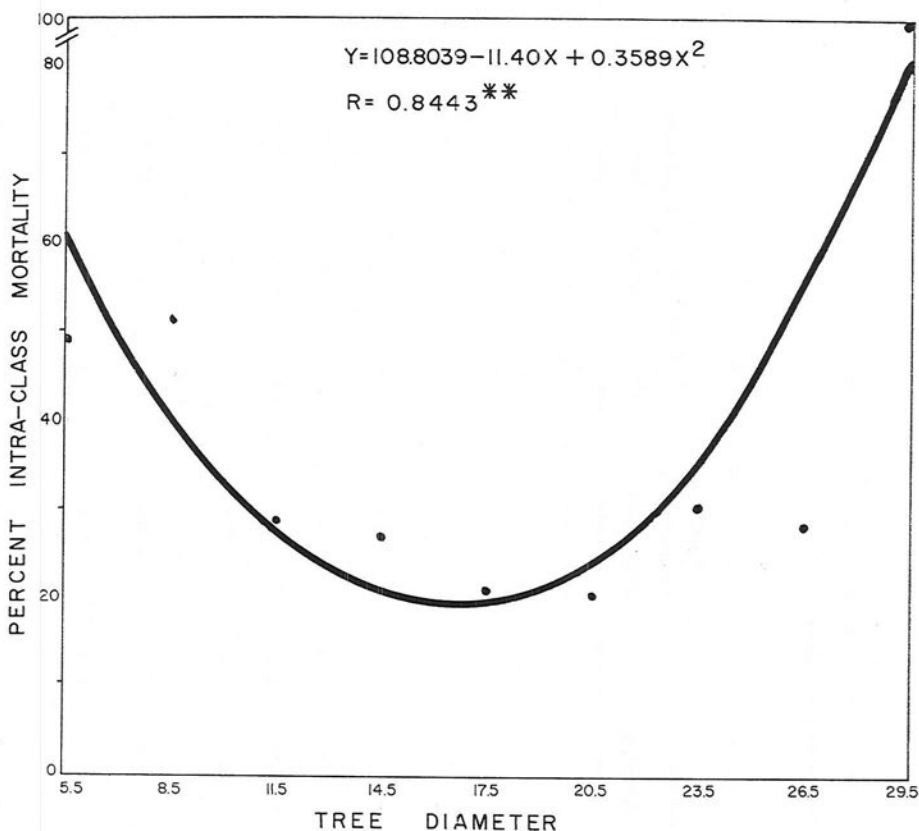
The decrease in importance of the leading dominant necessarily increased that of the remaining less tolerant trees, resulting in an alteration of stand continuum index of only 2.5%. Within the sapling regime, sugar maple so outweighed all other species that, even though one-half of them died, the upgrading of sapling size species other than maple was inconsequential. Saplings were represented by 6 species, whereas trees were represented by twice that number.

Table 8 reveals the hierarchy of relative importance of species in stand 3. Sugar maple trees declined 9.3% in relative importance, while all others increased.

In addition to mortality information, crown defects were qualitatively evaluated

Part I, Table 5. Characterization of mixed northern hardwood stands following development of maple blight.

Stand no.	Relative importance value of tree species						Relative importance sugar maple saplings	Trees per acre		Continuum index trees
	Sugar maple	Hemlock	Yellow birch	Basswood	American elm	Others		All trees	Sugar maple	
7	34.8	22.4	10.6	5.7	7.4	19.1	77.9	79	25	2,644
6	48.3	17.7	12.7	3.9	6.1	11.3	63.4	120	61	2,708
8	32.9	23.9	16.2	6.0	13.1	7.9	83.4	116	42	2,605
4	46.7	21.5	10.3	3.5	9.1	8.9	49.4	132	65	2,688
2	44.6	15.7	9.5	8.0	14.9	7.3	62.7	167	80	2,650
3	26.0	27.3	15.5	3.4	14.9	12.9	73.9	107	34	2,546
5	33.9	23.8	18.8	7.4	6.1	10.0	39.3	211	63	2,610
Total	267.2	152.3	93.6	37.9	71.6	77.4	450.0	932	370	18,451
Mean	38.2	21.8	13.4	5.4	10.2	11.1	64.3	133	53	2,636



Part I, Fig. 4. The intra-class relative mortality of sugar maple trees in blighted stands (based on 3482 samples; diameter intervals mark the midpoints of 3-inch size classes.)

in the 1960-61 studies of stand 3. All living individuals were classified broadly into *unaffected* and *affected* (most probably by maple blight). Of the approximately 50% (798) maple saplings still living, 96.6% showed symptoms; only slightly more than 3% were unaffected. Of the 47% maple trees remaining, 97.9% (143) had deteriorating crowns.

The elimination of numerous trees and saplings of sugar maple by maple blight over vast areas in central Florence County resulted in large openings in the canopy. In most blighted stands, nearly full sunlight prevailed, in contrast to the normal situation where often less than 100 foot-candles were available beneath the dense canopy. This increased solar radiation enhanced a lush growth of weeds in many areas. Such plants as those listed in Table 9

have been termed "increasers". Of the eleven plants determined, only *Osmorhiza claytoni* and *Circaea alpina* are listed by Curtis (1959) as prevalent groundlayer species of the northern mesic forest. The remainder are modal in communities other than the northern mesic; some are true weeds. The great increase in populations of weedy groundcover plants is truly indicative of a disturbed situation.

Besides the current economic loss and the destruction of large numbers of maple saplings, which would have been the future dominants, maple blight incurred an even greater influence on the diseased stands. The change of forest type resulted in an increase in importance values of the less shade tolerant tree species such as hemlock, ironwood, American elm, yellow birch and basswood in the tree sizes.

Part I, Table 6. Distribution of tree and sapling mortality of sugar maple in blighted stands.

Stand	Mortality (percent)	
	Tree	Sapling
2	5.0	12.5
3	23.7	56.2
4	11.5	40.6
5	1.9	0.6
6	11.2	49.4
7	33.1	32.5
8	20.0	39.4
Total	106.4	231.2
Mean	15.2	33.0

Part I, Table 7. The distribution and mortality of sugar maple trees in maple blighted stands.

Diameter ¹	Relative distribution	
	All trees, pre-blight ²	Dead trees, post blight ³
2.5	75.4	78.1
5.5	12.9	13.7
8.5	2.6	2.9
11.5	1.9	1.2
14.5	1.9	1.1
17.5	2.2	1.0
20.5	1.7	0.8
23.5	0.9	0.7
26.5	0.4	0.3
29.5	0.1	0.2

¹ Midpoints of 3-inch size classes.

² Based on 3482 samples of living and dead trees (pre-blight) within blighted stands.

³ Based on 1601 samples of dead trees.

Generally, in the sapling class, ironwood and American elm attained greater importance following the blight; neither of these species is especially desirable from an economic standpoint. The increased importance of the less tolerant species, consequently, has lowered the value of the stand continuum indices also, and the stands have regressed on a successional scale from a point of high stability to a situation where one or more of several events will occur: (1) the stands may continue with sugar maple as the high relative importance species, (2) the already modified environment established

by the previous climax stands may give rise to gap phase tree species or (3) the successional pattern may revert back to a semi-pioneer situation. A combination of the last 2 possibilities will probably occur. Even though an abundant supply of maple seedlings was still available in 1961, it is doubtful that they will survive the spatial competition in the more severely denuded areas now heavily occupied with weeds.

Thirteen structural and behavioral attributes of the stands were tested against relative mortality; significance was demonstrated for 2 correlations. The relative importance of sugar maple saplings was

Part I, Table 8. Characterization of mixed northern hardwood stand 3 based on a 4.2 acre sample.

Species	Relative importance value				Trees per acre		Continuum index trees	
	Trees		Saplings		Pre blight	Post blight	Pre blight	Post blight
	Pre blight	Post blight	Pre blight	Post blight				
Sugar maple	38.8	29.5	78.8	74.7	68	32	1164	855
Hemlock	13.2	15.5	0.0	0.0	11	11	317	373
Yellow birch	14.1	16.7	2.0	2.2	12	12	339	401
Basswood	4.2	4.8	2.5	2.9	3	3	101	115
American elm	15.4	17.9	8.4	10.0	11	11	369	430
Others	14.3	15.6	8.3	10.2	16	16	316	367
Total	100.0	100.0	100.0	100.0	121	85	2606	2541

Part I, Table 9. Herbaceous increasers in blighted stands.¹

Species	Common name
<i>Aster puniceus</i> L. ²	Aster
<i>Circaea alpina</i> L.	Enchanters nightshade
<i>Cirsium arvense</i> (L.) Scop.	Canada thistle
<i>Erigeron ramosus</i> (Walt.) BSP.	Daisy fleabane
<i>Galeopsis tetrahit</i> L.	Common hemp
<i>Lactuca pulchella</i> (Pursh) D.C.	Blue lettuce
<i>Lappula virginiana</i> (L.) Green	Stickseed
<i>Osmorhiza claytoni</i> (Michx.) Clarke	Sweet cicely
<i>Rubus</i> sp.	Raspberry
<i>Urtica gracilis</i> Ait.	Nettle

¹ Determined by Prof. A. L. Throne, University of Wisconsin, Milwaukee.

² Authority—Robinson and Fernald, 1908.

positively and significantly correlated with percentage mortality of sugar maple saplings ($r = 0.769^*$; $y = 0.849x - 26.8$) (Table 10). Behaviorally, this suggests that the greater the importance of sugar maple in the sapling stage from the standpoint of distribution and numbers, the more susceptible the stand was to maple blight.

The mean relative density of sugar maple trees and saplings was positively and significantly correlated with relative mortality ($r = 0.710^*$; $y = 1.006x -$

41.37). Structurally, this suggests an increasing susceptibility of the stand to maple blight with increasing numbers of sugar maple trees and saplings relative to the other species.

Eleven of the 13 characters tested yielded no significance; however, the signs of the regression coefficients reveal important trends. In general, tree and sapling relative mortality increased with increasing relative importance of trees and saplings. The percentage of dead maple increased with increasing numbers

Part I, Table 10. Correlations of stand factors within maple blighted stands.

Stand factor (X)	Mortality of indicated individuals (percent) (Y)	Regression coefficient
Mean relative density of maple saplings and trees	Saplings and trees	+1.006*
Relative importance of maple saplings	Saplings	+0.849*
Mean relative frequency and density of maple saplings and trees	Saplings and trees	+0.550
Mean importance value of maple saplings and trees	Saplings and trees	+0.218
Sugar maple saplings per acre	Saplings and trees	+1.742
Sugar maple saplings per acre	Saplings	+0.111
Sugar maple saplings per acre	Trees	+1.572
Number of trees (all species) per acre	Saplings and trees	-0.477
Number of trees (all species) per acre	Saplings	-0.638
Number of trees (all species) per acre	Trees	-0.287
Basal area (all species) per acre	Saplings and trees	-0.347
Basal area (all species) per acre	Saplings	-0.440
Basal area (all species) per acre	Trees	-0.188

* Significant at 0.05 probability level.

of maple saplings in a unit area. Increasing numbers of trees (unit area; all species) were inversely related to maple relative mortality. All species basal area also was negatively correlated with relative death of all sizes of maples. None of these factors taken alone was invariably implicated; an interaction of all factors is a more reasonable hypothesis. The stand characteristics are probably much more important biologically and silviculturally than could be demonstrated statistically with the small number of blighted stands.

An Interstand Ordination of Maple Study Areas

All stands were compared by determining indices of similarity (Bray and Curtis, 1957). The relative values of frequency, density and dominance of the trees and frequency and density of the saplings were used as quantitative characters for all

tree species. The degree of phytosociologic similarity ranges theoretically from 0 to 1.0, representing no and complete commonness respectively. The inverses of similarity coefficients (dissimilarities) were determined so that stands with least in common were represented by the greatest spatial separation.

An ordination in 3 dimensions was constructed following the technique described by Beals (1960). No reference stands of a given axis were reused as references for another axis; the absolute axis length used was the interpoint distance between the high and low reference stands. Since axis lengths so defined are variable in length, the stands were assigned the same relative positions on an expanded (0-100) axis in accordance with the format established by Burgess (1959).

The ordination is based on information from the stand as it existed prior to the development of maple blight. If a phytosociologic predisposition is hypo-

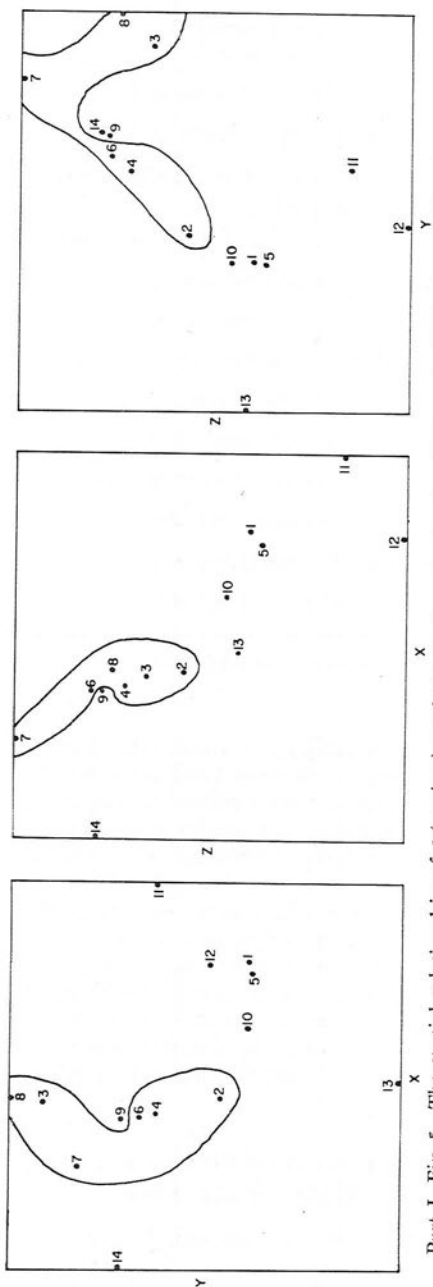
thesized, then pre-disease conditions must be studied. Hence the point position of each stand is derived from preblight factors (Fig. 5). The diseased stands fall into a neat cluster on all three axis pairs with the addition of stand 9, a non-diseased stand (although similar in all structural and compositional attributes this stand is one of the farthest geographically and had no epiphytotic insect populations present).

To interpret ordination with greatest meaning, the stands should be observed as a constellation in three dimensional space rather than points on a line or on a two-axis plane (E_2). Figure 6 shows a model of such a constellation viewed obliquely. When inter-stand distances are determined for the constellation, diseased stands are generally more closely associated (spatially) with each other than with non-diseased stands. That is, the maple-blighted stands form a quite discreet group.

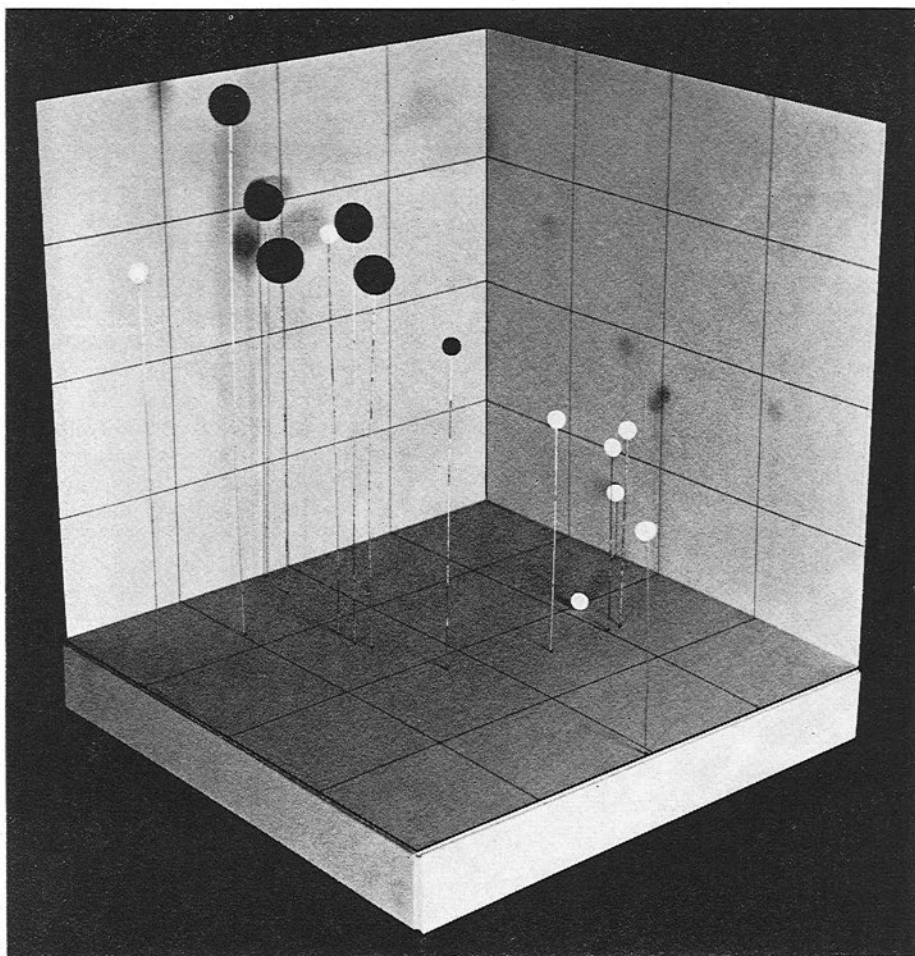
Stand positions on individual axes may be related to plant behavioral attributes with the use of correlation analyses. Many trends were apparent, however, several are of special consequence. Two factors were significantly related to the stands on the x axis. Total unit area basal area is positively correlated on the x axis (where $b = +0.7244$; $r = 0.563^*$) and relative importance of sugar maple trees and saplings is negatively correlated on the same axis ($b = -0.1625$; $r = 0.546^*$). The diseased stands are oriented towards the lower extreme of the primary axis and are, therefore, associated with the low dominance (size) and high species importance of sugar maple. Relative importance of sugar maple was also correlated on the y axis with high significance ($b = +0.2038$; $r = 0.682^{**}$); on this secondary axis, the maple blighted stands lie towards the high extreme.

The ordination technique provides a useful approach for insect and disease ecology and their perplexing association with silviculture. With such a mathematical device, complex information may be sorted into meaningful units that can be studied.

No single vegetational factor of all



Part I, Fig. 5. The spatial relationship of 14 upland northern hardwoods stands within each of the three ordination views. Diseased stands are included within the contours.



Part I, Fig. 6. Constellation of upland northern hardwoods stands based on an ordination derived from structural and compositional data prior to the advent of maple blight. White circles represent non-diseased stands. Black circles represent diseased stands with circle diameter being proportional to mortality as follows: smallest, 6-20 percent; medium, 21-35 percent; largest, 36 percent or greater mortality. The primary (x) axis lies on the lower right horizontal plane of the figure and increases to the right. The secondary (y) axis is also the horizontal plane but the lower left portion and increases from front right to back left. The tertiary axis (z) increases upwards in the vertical plane.

maple blighted stands could be identified as a predisposing agent to maple blight. Maple blight appeared rather as a response to a multifactoral cause. Generally, the areas subjected to heavy losses were characterized by high importance of maple and low basal areas relative to all stands studied. None of these factors taken alone, how-

ever, was invariably incriminated; an interaction of all factors is much more reasonable. These correlations also suggest that stand conditions were related to maple blight through other biotic factors. In the following sections of this bulletin, the role of biotic agents in the genesis of maple blight will be presented.

Summary

A new disease, referred to as maple blight, was reported in Florence County, Wisconsin, in 1957 on lands with a history of intensive and selective logging and severe insect defoliation for several years previously. Characteristics of maple blight include branch dieback, foliage chlorosis and wilt, epicormic sprouting and tree mortality. The cooperative research program initiated by the University of Wisconsin, The Wisconsin Conservation Department and the Lake States Forest Experiment Station was designed to investigate the entomological, pathological and ecological factors related to the genesis of the disease.

Ecologically, the general blight area is included in the northern conifer-hardwood province characterized by low temperatures and short growing seasons. Sugar maple is the potential dominant species with hemlock, yellow birch, basswood, American elm and a number of other shade tolerant species in the association.

The relationship between forest characteristics and the occurrence of maple blight was investigated in seven non blighted stands and seven blighted stands prior to and after the appearance of the disease. Point sampling was employed in the derivation of relative importance values for trees and saplings and tree continuum indices.

Stands in which blight occurred were similar to adjacent non blighted stands based on evaluation of relative importance values and continuum indices. Following the occurrence of blight, sugar maple trees declined in relative importance although they continued to be the leading dominant. Sugar maple saplings also declined slightly in relative importance. Mortality of trees averaged 15.2% and that of saplings 33.0%. The distribution of tree mortality in absolute terms declined curvilinearly from the smallest to the largest size class reflecting a skewness toward the small diameter scale. Over 90% of the trees that died were less than 11 inches in diameter. However, analysis

of the relative number of individuals within size classes demonstrated that suppressed and overmature trees were affected more severely than were intermediate trees.

Maple blight resulted in an opening of the stands allowing nearly full sunlight to reach the forest floor. This increase in solar radiation enhanced a lush growth of weeds that reflected the intensity of the disturbance of the forest itself.

In the blighted stands hemlock, ironwood, American elm, yellow birch and basswood trees increased in importance value. In the sapling classes ironwood and American elm showed increases. It is postulated that because blight has caused a regression on the successional scale from a point of high stability, one or several of the following events may occur:

- a. The stands may continue to develop with sugar maple as the high relative importance species.
- b. Gap phase species may become dominant.
- c. The successional pattern may revert back to a semi-pioneer stand.

Thirteen structural and behavioral attributes of the stand were tested against relative tree and sapling mortality. The relative importance of sugar maple saplings was significantly correlated with percent mortality suggesting that stands with greater numbers and distribution were more susceptible to blight. Also the mean relative density of sugar maple trees and saplings was significantly correlated with relative mortality. Structurally and compositionally this suggests an increasing susceptibility to blight with increasing numbers of sugar maple trees and saplings relative to other species. The mathematical and graphic technique of three dimensional ordination demonstrated that prior to blight the diseased stands fell into a discrete grouping.

No single vegetational factor of all maple blighted stands could be consistently identified as a predisposing agent

to maple blight. Maple blight appeared rather as a response to a multifactoral cause. Generally, the areas subjected to heavy losses were characterized by high importance of maple and low basal areas relative to all stands studied. None of these factors taken alone, however, was invariably incriminated; an interaction of

all factors is much more reasonable. These correlations also suggest that stand conditions were related to maple blight through other biotic factors. Most prominent of these was insects as all maple blighted stands were characterized by prior epiphytotics of a complex of defoliating Lepidoptera.

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Part II. The Insect Complex Associated With Maple Blight

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PART II.

The Insect Complex Associated With Maple Blight¹

Ronald L. Giese² and Daniel M. Benjamin³

Introduction

STANDS WITH MAPLE BLIGHT had been attacked previously by high populations of defoliating insects. This was true on a spatial basis, and also by a coincidence in time. That insects, through their defoliating activities, were related somehow to maple blight was strongly suggested by these circumstances. In the early stages of the maple blight epiphytotic, however, much skepticism was expressed concerning the role of defoliating insects. It was suggested that defoliation by insects had no major detrimental influence on the trees and particularly no relationship with maple blight. This reflected the viewpoints of Craighead (1950) who expressed the general opinion that,

"Many years' observations on various hardwoods have shown that deciduous trees can stand as many as 5 to 10 years' defoliation, depending on site and previous vigor, before they succumb." Graham (1952) also stated that, "Hardwoods are relatively resistant and will successfully withstand 3 or more years of defoliation."

Despite the general view that sugar maple suffered little damage from insect defoliation, the role of these organisms needed to be investigated. The entomological study was initiated in 1958 to determine the relationships between the complex of maple defoliating insects and the genesis of maple blight.

The Leaf Roller, *Sparganothus acerivorana* MacKay

The leaf roller, *Sparganothus acerivorana* MacKay, was the first species to appear during the growing season in the

maple defoliator complex. The host list of this roller includes sugar maple, *Acer saccharum* Marsh.; red maple, *A. rubrum*

¹ This project was supported in part by the Northern Hardwood and Pine Manufacturers Association, the Wisconsin Conservation Department and the U.S. Forest Service, Lake States Forest Experiment Station; to these agencies, the authors wish to express their appreciation. Approved for publication by the Directors of the Wisconsin and Purdue Agricultural Experiment Stations.

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L.; silver maple, *A. saccharinum* L. and mountain maple, *A. spicatum* Lam. (MacKay, 1952). Sugar maple was the only host observed in Wisconsin and this is the first record of *S. acerivorana* here; this species has been recovered from Florence, Door, Iron and Langlade Counties.

Life Stages

The following description is taken from the original (MacKay, 1952). The ultimate larval instar length averages 21 mm; the head width averages 1.85 mm (146 last instar larval headwidth measurements by the authors yielded a mean of 1.79 mm). The body color is yellowish-green. The prothoracic shield is tan and is edged with a continuous distinctive brown or black band (Fig. 1). The mean wing expanse of the males is 21.8 mm; that of the females is 23.8 mm. The adult forewings are barium yellow; the posterior wings and the abdomen are white.

Life History

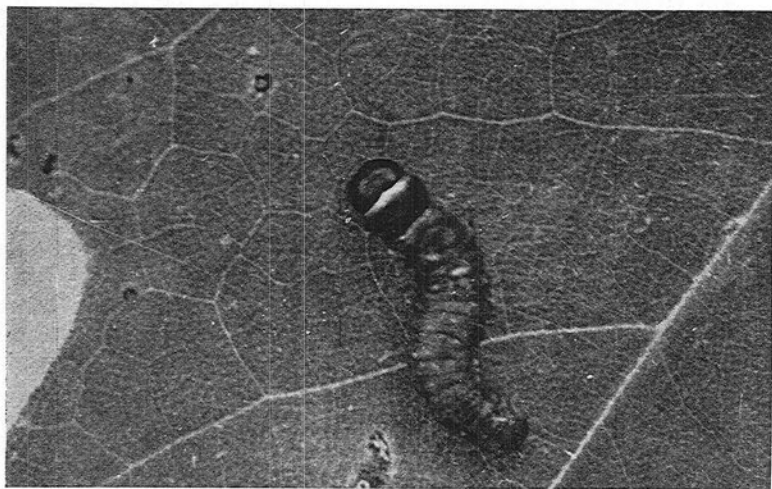
Larvae. The larvae of *S. acerivorana* are solitary feeders found, when at rest, within rolled maple leaves. Over 80% of 500 rolled leaves examined in 1958 had the lower surface rolled. The completed roll of this species is conically shaped (Fig. 2). Larvae utilize the roll

only as a retreat (and later for pupation); feeding takes place on adjacent leaves.

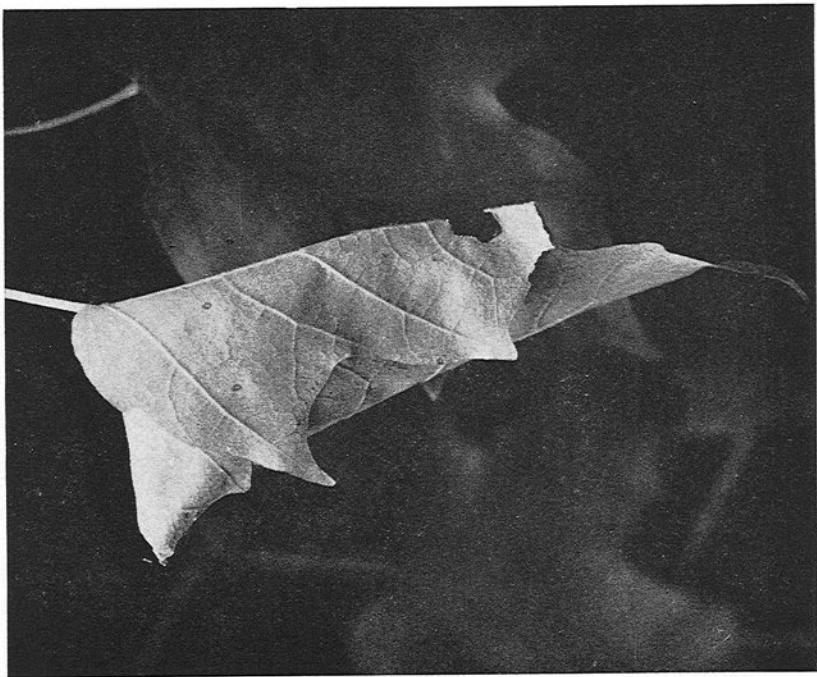
Leaf rolling. The technique of leaf rolling was studied in the laboratory and corroborated by field observations. At the start of the rolling process, the larva lays a layer of silk about 1 inch in length and $\frac{1}{2}$ to $\frac{3}{4}$ inch wide on the lower side of the primary leaf lobes; the process requires 6 to 10 minutes for completion. Although the silken layer later serves as a retreat and pupal chamber, it functions first as a roll initiator. When the layer has been completed, the leaf is noticeably curved in a plane perpendicular to the silk threads.

The next step involves the construction of several main spans. The first main span is begun at the smallest tip of a main leaf lobe and at the anterior end of the silken layer. Silken threads are laid from the leaf margin to the middle lobe surface during a side-to-side motion of the head and anterior part of the caterpillar. Each main span is comprised of several hundred short lengths of silk. As many as 54 one-half inch lengths can be spun per minute.

The silk contracts upon drying and, consequently, each successive length in a given main span becomes shorter. Likewise, each successive column or main span becomes shorter than the previous. This explains the process of leaf rolling in



Part II, Fig. 1. The larva of *Sparganothus acerivorana*.



Part II, Fig. 2. Sugar maple leaf completely rolled by *Sparganothus acerivorana*.

which spinning, drying and contraction of the silk pulls 2 surfaces of the leaf together.

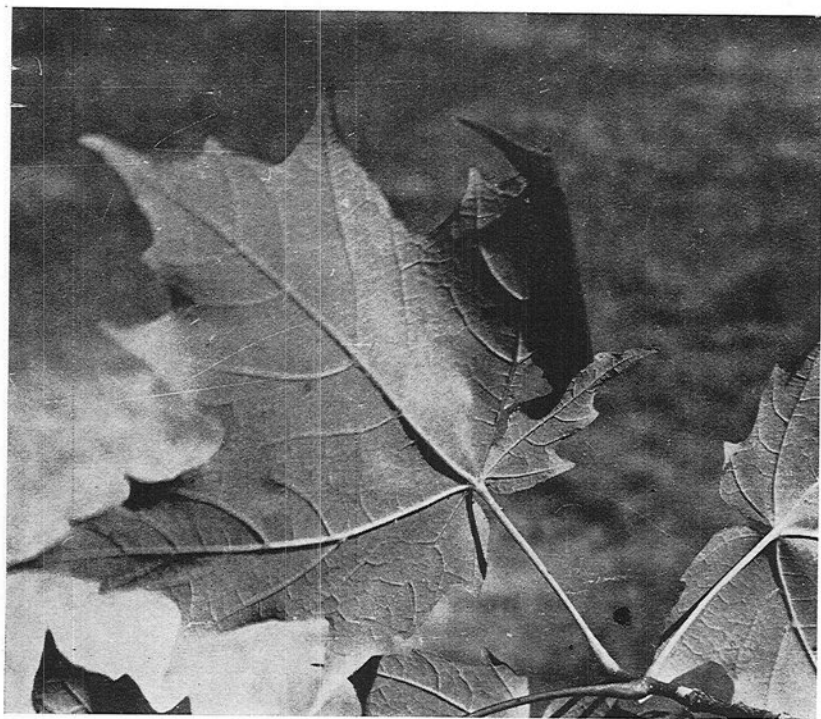
As many as 4 main spans may be spun; each new span is located progressively nearer the central portion of the leaf and causes the leaf to roll as the silk-layer and first main spans contract. With the completion of the main spans, the leaf margin is nearly doubled over and rests about $\frac{1}{8}$ inch above the central portion of the leaf (Fig. 3). The larva then retreats to the inside of the chamber and spins a general mesh of threads the length of the interior roll causing the leaf margin to rest on the central leaf surface.

Further rolling is effected by spinning and attaching silk to the top of the roll and central leaf surface alternately (Fig. 4). As the curling tends to become easier once the roll has been started, the main spans are constructed successively farther back towards the petiole. In most instances, this gives rise to a conical structure rather than a cylinder. The completely rolled leaf may contain as many as ten secondary spans of silk.

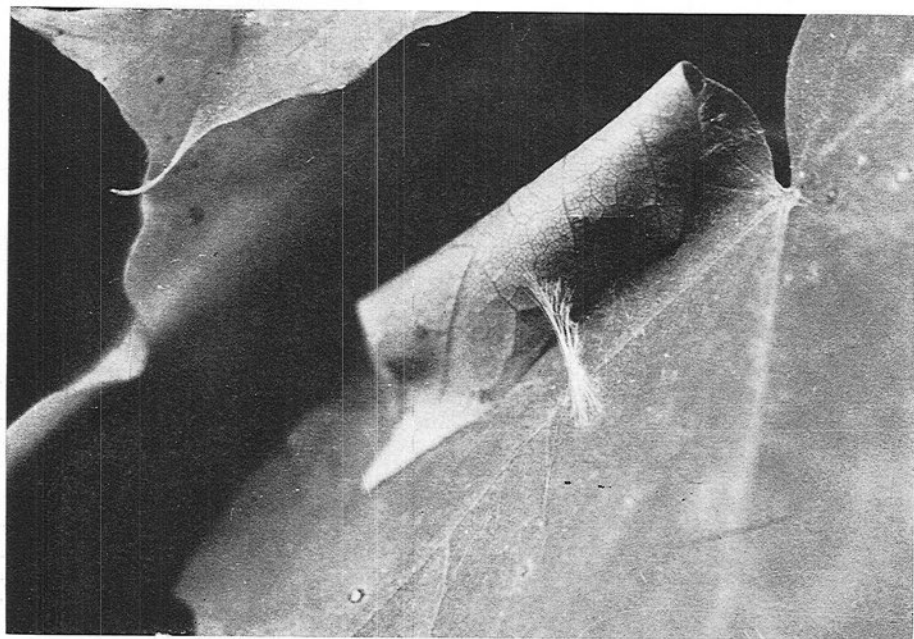
Frequently, the basal end of the rolled leaf is folded over to almost completely close off that orifice. A small opening remains, however, which the larva uses as an exit and entrance to the shelter. The rolled leaves are not fed upon by the larvae. Occasionally, rolls were observed that, when completed, had a $\frac{1}{4}$ to $\frac{1}{2}$ inch ledge remaining. This ledge is important to the webworm association to be discussed later.

Mature larvae occupy that portion of the roll which served as the original fold. Except for one edge, this fold is separate from the remainder of the roll and forms a purse-shaped retreat and pupal chamber.

About a month after construction of the roll is completed the leaves become non-functional, the main veins break, the leaves yellow, the abscission layer forms and leaves detach readily. Vein breaking that results in premature abscission is a weak link in the life cycle of *S. acerivorana*. The driving force of June and July rains with accompanying winds were of sufficient magnitude in 1958 to detach most of the older rolled leaves from the



Part II, Fig. 3. Completed first stage roll of *Sparganothus acerivorana*.



Part II, Fig. 4. Column type of leaf rolling by *Sparganothus acerivorana*.

twigs. Following such storms, the ground was covered with detached rolls, and several days later, the larvae in them were usually dead.

Larval host selection. A larval host selection study was conducted, utilizing 60 larvae in each of 2 trials of an arena type experiment. Five freshly severed leaves of each of 5 tree species were arranged in circles, so that each leaf of a given species was adjacent to one of a different species. The larvae were placed in the center of the arena. After 12 hours, examinations were made for leaf rolling, the criterion for selection. Two trials revealed that 78% of the larvae satisfied the rolling criterion and these were distributed as follows: basswood, 25.4%; sugar maple, 23.4; yellow birch, 19.1; ironwood, 16.0; red maple, 10.6; and American elm, 5.5. Thus, it is possible for *S. acerivorana* larvae to roll leaves of species other than those of sugar maple. Although it is not the initial prerogative of larvae to select the host, chance disturbance often results in dropping from the original host to one below which may be a different species. If this insect can roll and feed on species other than those on which eggs were deposited, a selective survival advantage would be afforded.

Pupae and adults. Pupation takes place in the purse-shaped chamber of the rolled leaf. In Wisconsin, pupation occurred in late June through early July (Table 1). Transformation to the adult occurred in late July; mating and oviposition took place in the same season. In Quebec, pupation and adult emergence begin in late June and continue through early July (MacKay, 1952).

Natural Control

Twenty primary parasitic Hymenoptera have been reared from *S. acerivorana* larvae and pupae (Table 2). Of these *Apanteles polychrosides*, *Mesochorus sylvarum*, *Meteorus trachynotus*, *Microgaster epagoges* and *Phaeogenes* sp. (in order of their importance) comprised over 83% of all parasitoids.

Spiders reduced larval populations of the leaf rollers more than all other predators combined. *Clubiona* sp. and *Xysticus elegans* (Keys) were most commonly encountered, and caused nearly 1/3 of the larval mortality. The pentatomid, *Podisus placidus* Uhler, was infrequently collected, but when present, was an effective control agent. A single adult was observed to kill 10 leaf rolling larvae per day.

Part II, Table 1. Observation dates of three life stages of *S. acerivorana* in 1958 and 1959.

Stage	1958		1959	
	Date observed		Date observed	
	first	last	first	last
Larval	V - 20	VII - 6	-	VII - 22
Pupal	VII - 4	VIII - 3	VI - 22	VII - 22
Adult	VII - 23	VIII - 4	VII - 22	VII - 24

The Leaf Roller, *Acleris chalybeana* (Fernald)

The second major leaf roller to appear in the seasonal succession of the sugar maple defoliator complex was the tortricid, *Acleris chalybeana* (Fern.). Fernald (1882) placed this species in the genus

Teras after study of adults of both sexes collected in 1880. Subsequently, *chalybeana* was transferred to *Peronea*, then to *Olethreutes* (Dyar, 1902) and finally to the presently accepted *Acleris* (Forbes, 1925).

Part II, Table 2. Hymenopterous parasitoids associated with *Sparganothus acerivorana* and *Acleris chalybeana* in Florence County, Wisconsin.

Parasitic species	Parasitizing		<i>Sparganothus acerivorana</i>	<i>Acleris chalybeana</i>
	larva	pupa		
<u>Primary parasitoids</u>				
Braconidae				
<i>Apanteles clavatus</i> (Prov.)	+			+
<i>Apanteles plesius</i> Vier.	+		+	
<i>Apanteles polychrosides</i> Vier.	+		+	+
<i>Apanteles</i> sp.	+		+	+
<i>Ascogaster</i> sp.	+		+	
<i>Clinocentrus</i> sp. (appar. new)	+		+	
<i>Meteorus argyrotaeniae</i> Joh.	+			+
<i>Meteorus hyphantriae</i> Riley	+			+
<i>Meteorus trachynotus</i> Vier.	+		+	+
<i>Microgaster epagoges</i> Gah.	+		+	+
<i>Microgaster peroneae</i> Wall.	+		+	+
<i>Microgaster</i> sp. near <i>peroneae</i>	+			+
<i>Oncophanes americanus</i> (Weed)	+			+
<i>Oncophanes betulae</i> Mues.	+			+
Eulophidae				
<i>Pediobius niger</i> (Ashm.)		+		+
<i>Pediobius sexdentatus</i> (Grlt.)		+		+
Ichneumonidae				
<i>Acrolyta</i> sp.? <i>longicornis</i> (Frov.)	+		+	
<i>Acropimpla alboriota</i> (Cress.)	+		+	
<i>Alegina</i> sp.	+			+
<i>Eclytus pleuralis</i> (Prov.)	+		+	
<i>Exochus</i> sp.	+			+
<i>Horogenes</i> sp.	+		+	+
<i>Leropus coelebs</i> (Walsh)	+	+	+	+
<i>Lioplectus conquisitor</i> (Say)	+	+	+	+
<i>Mesochorus sylvarum</i> Curt.	+		+	
<i>Mesochorus</i> sp.	+		+	+
<i>Phaeogenes</i> sp. (prob. new)		+	+	
<i>Scambus hispae</i> (Harr.)	+			+
<i>Scambus</i> sp.	+		+	+
<i>Syrphoctonus</i> sp.	+		+	
Perilampidae¹				
<i>Perilampus fulvicornis</i> Ashm.	+		+	
<u>Hyperparasites²</u>				
Elasmidae				
<i>Elasmus pullatus</i> How.			+	+
Eulophidae				
<i>Dimmockia pallipes</i> Mues. ¹			+	
<i>Pediobius tarsalis</i> (Ashm.) ¹			+	+
Pteromalidae				
<i>Hypopteromalus inimicus</i> Mues.			+	

¹ Species emerged from larvae and pupae and may be hyperparasites.

² All hyperparasites were associated with larval primary parasitoids of the indicated species.

This species has been taken in California, Maine, New York, Oregon and Pennsylvania (Dyar, 1902; Fernald, 1882; Forbes, 1925). The discovery of *A. chalybeana* in Wisconsin marks the first record of this insect in the Lake States; it has been observed commonly and collected in Door, Florence, Forest, Iron, Oneida and Shawano Counties.

The host list for this species in north-eastern and north-central Wisconsin is: sugar maple, red maple, mountain maple, ironwood, and yellow birch.

Life Stages

Larvae. The larva of *A. chalybeana* ranges in length from 2 mm in the first to 22 mm in the ultimate stage. The internal structures of the larva lend an appearance of irregular shading. It is light green and the cuticle enveloping the meso- and metathorax and the abdomen is uniformly colored. The characteristic most useful for differentiating this larva from others in the complex is the prothoracic shield. This structure has black lateral posterior

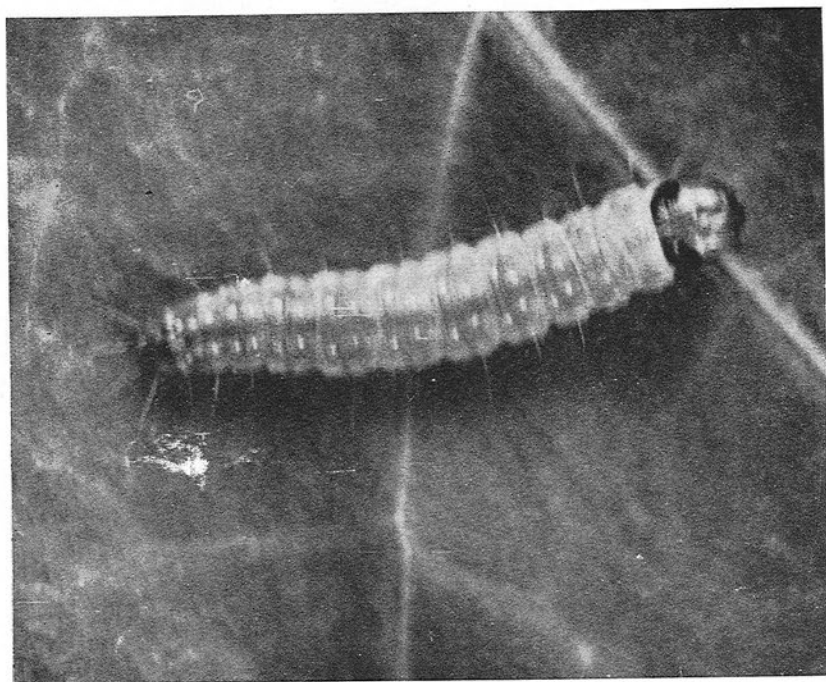
corners while, from the dorsal aspect, the shield appears to have a discontinuous black band at the posterior end at a right angle to the long axis of the larva (Fig. 5). Six larval stages were defined from 534 head capsule measurements (Table 3).

Pupae. Pupae of *A. chalybeana* are typically exarate, dark brown and range in length from 8.0 to 11.0 mm.

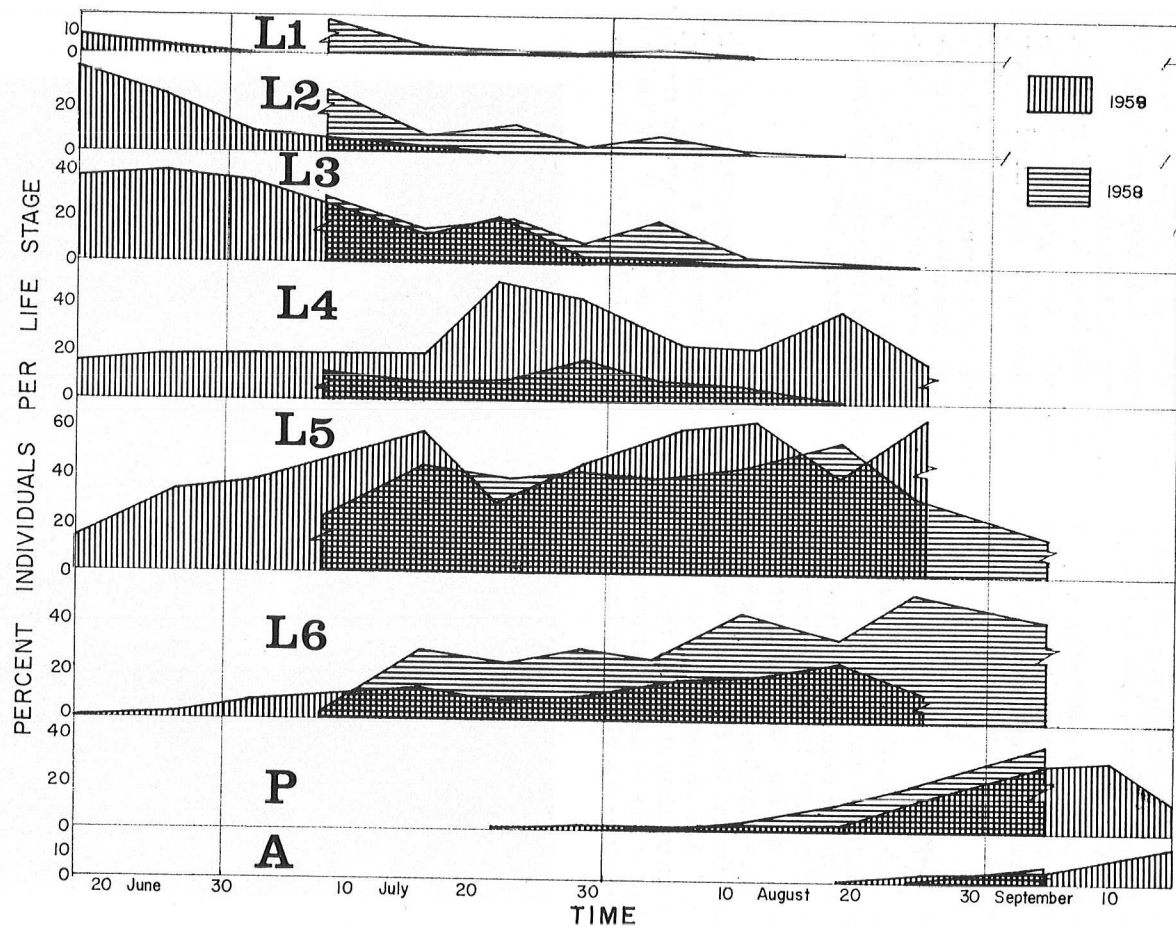
Adults. The imago is a small moth; the general body color is grey. The forewings are grey and have an expanse of 22 mm; the posterior wings are cream-colored with fringes of a lighter shade. "A small black band extends from the costa at the base of the wing partially across, forming, when the wings are closed, a continuation of the transverse black band of the thorax" (Fernald, 1882).

Life History

Larvae. Larvae first appeared from early to mid-June during 2 growing seasons (Fig. 6). Although the specific site of over-wintering in nature is not known, laboratory tests indicated that first or sec-



Part II, Fig. 5. Fifth instar larva of *Acleris chalybeana*.



Part II, Fig. 6. The distribution of life stages of *A. chalybeana* over two growing seasons. (The 1959 curves represent 1264 specimens; those of 1958 include 1087). L1 to L6 indicate larval instar, P—pupal, and A—adult stage.

ond instar larvae issued from hibernacula on the young twigs.

In 1958, the greatest proportion of *A. chalybeana* larvae appeared first as inquilines in abandoned rolls formed by *S. acerivorana*. The protection and nourishment of the roll obviated the formation of rolled leaves by the young larvae. Abandoned rolls of *S. acerivorana* were particularly useful from the standpoint of food mass as *S. acerivorana* did not feed within the roll. By contrast, *A. chalybeana*, a solitary form, fed within the roll. After several weeks of feeding, the nutritive resources were exhausted. The larvae then attached the dead rolls to adjacent new leaves (Fig. 7), fed for several more weeks and finally rolled single new leaves. In 1959, this phenomenon was only rarely observed because of the major decline of *S. acerivorana*.

Seasonal development was more rapid and advanced in 1959 than in 1958

(Fig. 6). In the third week of June, 1959, 75% of the larval population was in instars one, two and three. One month later, over 85% of the larvae were in the fourth, fifth and sixth stages. There was less growth in the fourth than in any other instar (Table 3). Since less time was occupied by this stage, it had less chance of being sampled and it would probably be represented in the population by relative numbers less than expected for theoretical development curves. In 1958, the early stages were last collected at dates much later than in 1959; in fact, larval stages one, two and three were collected for the last time 42, 26 and 14 days earlier in 1959 than in 1958. The development curves (Fig. 6) indicated peaking at an earlier date in 1959. In the later stages of development, however, some compensatory mechanism resulted in a reduction in time difference between the two seasons; the first dates of collection



Part II, Fig. 7. Roll of *Sparganothus acerivorana* being rolled into a new leaf by *Acleris chalybeana*.



Part II, Fig. 8. Row type rolling of *Acleris chalybeana*.

for the last stage larva, the pupa and the adult were respectively only, 6, 5 and 10 days later in 1958 than in the following season.

The roll, as an entity, demands qualitative and quantitative examination, for it predisposes maple for a defoliation phenomenon to be described later. While the process of rolling the leaf is essentially similar in both leaf rollers, the leaves rolled by *A. chalybeana* may be distinguished by three criteria: silk is spun in rows (Fig. 8), the completed roll is tubular, and only the lower surface is rolled, i.e. the lower epidermis lines the roll interior. A comparison of the rolled leaves and their inhabitants serves to distinguish the major leaf rolling species (Table 4).

Rolling of the leaves is generally initiated at one of the tips of one of the three main leaf lobes. This gives rise to three roll prototypes designated as roll types A, B and C (Fig. 9). Roll type A is initiated at the terminal lobe with the roll direction towards the petiole; type B begins at the ventral right and progresses to the left and type C is a

mirror image of B. The roll maintains, at completion, the directional form of its initiation as exemplified by the following: roll type A-1 gives rise to A-2 and A-3 at the 50 and 100% levels of leaf rolling respectively; roll type B-1 yields B-2 and B-3 upon further rolling; roll type C-1 ultimately becomes C-2 and finally C-3 (Fig. 9).

The selection of the site of rolling on the leaf is not random. Chi-square examination of data from 3,571 rolled leaves for a 1:1:1 ratio of rolls on either lateral main lobe or the terminal main lobe resulted in significant or highly significant differences, leading to a rejection of the 1:1:1 hypothesis. Chi-square tests for the same rolls revealed that a 3:1 ratio of any main lateral lobe to the terminal lobe fits adequately.

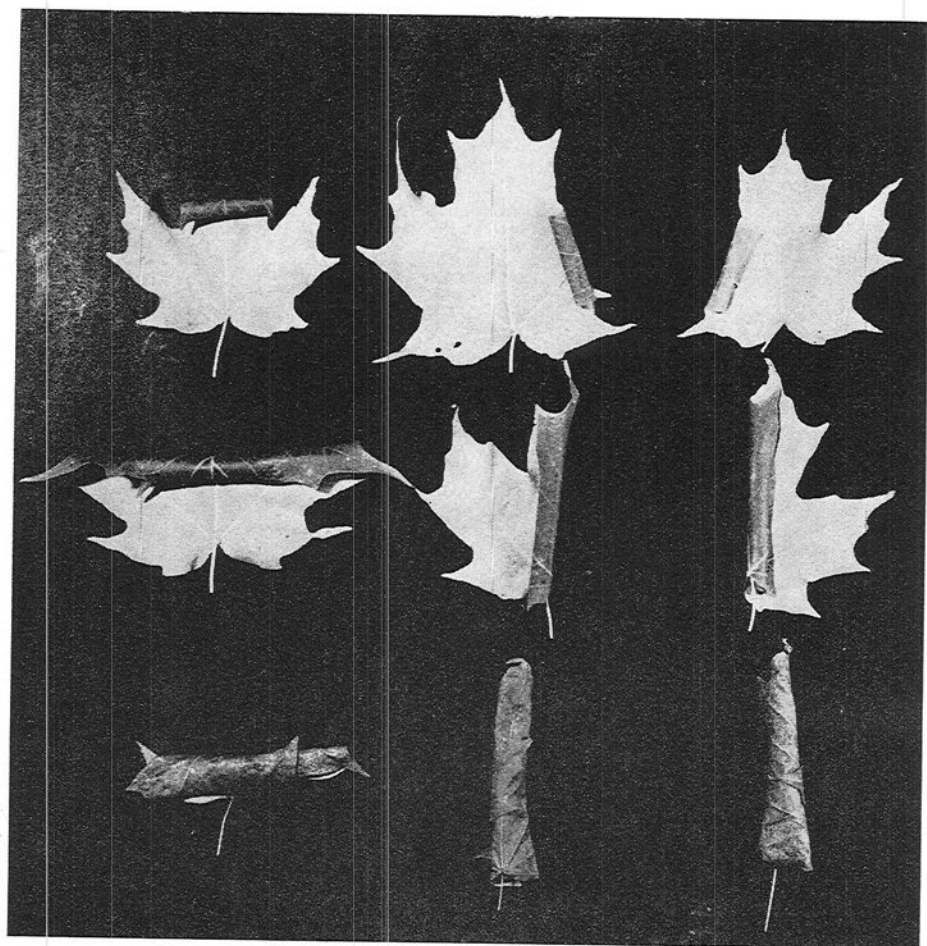
Laboratory tests with third, fourth, fifth and ultimate stages, demonstrated that when larvae were placed on the leaf, they usually rolled the surface on which they were placed, whether upper or lower. This is in contrast to populations in

Part II, Table 3. Head widths of the larvae of *Acleris chalybeana*.

Larval stage	Number	Actual mean width (mm)	s	range (mm)	Dyar ratio	Calculated width (mm)
L1	9	0.346	0.016	0.31-0.39	—	0.346
L2	84	0.476	0.083	0.40-0.55	1.38	0.465
L3	159	0.648	0.042	0.56-0.74	1.36	0.624
L4	95	0.785	0.036	0.75-0.85	1.21	0.838
L5	160	1.064	0.113	0.86-1.30	1.55	1.125
L6	26	1.502	0.064	1.31-1.61	1.41	1.511

Part II, Table 4. Characteristics for field separation of the major leaf rolling species of sugar maple in northeastern Wisconsin.

<i>Sparganothus acerivorana</i> MacKay	<i>Acleris chalybeana</i> (Fern.)	<i>Gracilaria</i> sp. prob. <i>packardella</i> Chamb.
Either surface rolled	Lower surface only rolled	Lower surface only rolled
Whole leaf involved in roll	Whole leaf involved in roll	Tips only rolled
One roll per leaf	One roll per leaf	One to five folds per leaf
No feeding on rolled leaf	Feeding common within roll; masked externally	Feeding within entire tip; externally visible
Pupal and retreat chamber constructed of leaf tissue	Pupal and retreat chamber constructed of frass	Pupa exposed on leaf in silken case
Webbing in columns	Webbing in rows	Webbing not visible
Larval prothoracic shield with dark posterior continuous band	Larval prothoracic shield with dark discontinuous band	Larval prothoracic shield without dark band
Pupa dark brown to black; naked	Pupa brown; naked	Cocoon: shiny, white



Part II, Fig. 9. Prototype rolls of *A. chalybeana*:

Left column: roll type A-positions 1, 2 and 3 (top to bottom),
 Middle column: roll type B-positions 1, 2 and 3 (top to bottom),
 Right column: roll type C-positions 1, 2 and 3 (top to bottom).

nature where in 2 years over 12,500 observations have revealed only lower surface rolling by *A. chalybeana*.

This predilection for the lateral main lobes and lower surface suggests that the young larvae, in a negatively geotropic response, crawl upwards from their hibernaculum to the nearest leaf. Once on the lower surface, they select the closest lobe to begin the rolling process.

Food demands increase as the larvae increase in size. This necessitates further rolling of the leaf to yield more food mass and to enable the larvae to feed in the seclusion of the unexposed leaf sur-

face. A highly significant correlation exists between the degree of leaf rolling (i.e. the percentage of any given leaf rolled) and the instar of the larva present in the same leaf. (The independent variable increases by Dyar's ratio rather than by the numerical increase of each larval stage.) The correlation coefficient of $+0.823^{**}$ was obtained from 154 samples; $y = 3.13 + 1.078x$. Thus, as the larvae increase in size, the leaves effectively become smaller because of increased rolling.

On a time scale (Table 5), the majority of leaves in the last week of June in 1959 were rolled only to the extent of 25%

Part II, Table 5. Degree of leaf rolling of *Acleris chalybeana* in 1959.

Month	Week	n	Percent of rolls with leaves rolled to indicated percent		
			25	50	100
June	4	41	68.3	24.4	7.3
July	1	517	51.8	39.4	8.7
	2	496	49.4	38.5	12.1
	3	427	34.9	44.7	12.6
	4	659	25.0	52.0	22.9
August	1	549	14.9	55.2	32.6
	2	298	14.1	54.4	31.5
	3	300	9.0	59.7	31.3
	4	295	9.8	62.0	28.5

n = Number of rolled leaves examined.

of the surface (including roll position 1 in roll types A, B and C). By the third week of July, the greatest single classification was represented by the 50% rolled class (position 2 of types A, B and C). In the last week of August, less than 10% were $\frac{1}{4}$ rolled, over 60% were $\frac{1}{2}$ rolled and nearly 30% were rolled to completion (100% roll includes position 3 of roll types A, B, and C).

The number of *A. chalybeana* leaf rolls on saplings was determined for the various study areas. In non-diseased stands, less than 130 *A. chalybeana* rolls per acre were present, while diseased areas supported populations ranging from 350 to 856 per acre. These data represent only insects on saplings. Larger trees support much greater populations of leaf rollers. Not only were total numbers greater in the diseased stands, but the mean number of rolls per sapling was significantly higher.

Pupae. Pupation of *A. chalybeana* took place in the rolled leaf, usually while the leaf was still intact. The specific site of pupation was within the frass chamber (Fig. 10). The pupal period for three newly pupated individuals was 15 to 18 days at a constant 68° F., 50% relative humidity and 12 hours of photoperiod.

Adults. Adults mated and females deposited eggs in the same season. In the laboratory, oviposition took place on sugar maple leaves. Nothing is known concerning fecundity, longevity or sex ratio of

adults. No adults were collected by black light traps operated during the flight period in areas of infestation.

Natural Control

Parasitism by mites, insects and pathogenic agents and predation by arthropods was recorded throughout the 1958 and 1959 seasons. Rolls formed by *A. chalybeana* were considered viable if they contained a larva or pupa; the larvae were recorded as dead, living or parasitized. Parasitized individuals included only those from which parasitoids had emerged; this statistic is *apparent parasitism*. This apparent phenomenon subjects the mortality data to errors due to the presence of endoparasitoids during the earlier periods; it becomes more accurate toward the season's end as the parasitoids mature and emerge. On a time scale, the presence of viable rolls and living population declined as the season progressed (Tables 6, 7 and 8). The occurrence of aphids and staphylinids (Table 6) will be discussed later.

Predation and apparent parasitism for the 1959 season exceeded 20% of over 9700 leaf rollers. The mortality of larvae in several areas exceeded 90% and the minimum adult emergence was less than 0.4%. Thus, the real mortality of immature *A. chalybeana* lies somewhere between 90 and 99%.

Part II, Table 6. Maple leaf roller defoliator complex in disease and non-disease stands in Florence County, Wisconsin. 1958.

Status of stand date	Percent <i>S. acerivorana</i>				Percent <i>A. chalybeana</i>			Percent habitation in any species roll by		
	n ¹	rolls	population alive	rolls viable	rolls	population alive	rolls viable	Aphids	Staphylinids	<i>T. asperatella</i>
Disease										
7/11	23	60.9	57.1	100.0	39.1	100.0	100.0	21.7	43.5	39.1
7/23	209	2.9	50.0	83.3	97.1	88.1	100.0	2.9	43.1	24.4
8/5	223	1.4	0.0	66.7	98.6	96.9	45.0	1.8	9.0	54.7
8/12	481	0.0	—	—	100.0	88.5	26.8	3.5	13.7	51.6
8/19	86	0.0	—	—	100.0	81.2	31.4	5.8	10.5	29.1
8/26	185	0.0	—	—	100.0	54.7	18.4	17.9	20.5	35.1
Non-disease										
7/4	331	100.0	60.8	95.4	0.0	—	—	39.3	26.0	1.2
7/11	107	100.0	32.4	98.1	0.0	—	—	33.6	4.7	13.1
7/18	211	19.9	10.5	74.9	80.1	96.5	100.0	15.2	1.9	33.6
8/2	79	0.0	—	—	100.0	87.5	60.8	19.0	5.1	5.1
8/13	272	0.0	—	—	100.0	81.8	32.3	13.2	7.7	4.8
8/6	161	0.0	—	—	100.0	68.3	28.6	16.0	0.0	0.0

¹ n=Number of rolled leaves examined.

Part II, Table 7. Leaf-roller dominance, mortality and webworm inhabitation in disease plots in Florence County, Wisconsin. 1959.

Date	n ⁴	Percent of rolls by		A.c. rolls viable	A.c. populations alive	Percent of rolls containing T.a. ³
		S.a. ¹	A.c. ²			
6/16	308	10.4	89.6	55.8	98.1	2.6
6/22	183	13.7	86.3	81.5	100.0	1.6
7/2	152	1.3	98.7	84.7	100.0	5.3
7/9	160	0.6	99.4	71.1	98.2	13.8
7/16	165	0.6	99.4	59.1	93.8	13.3
7/22	190	0.0	100.0	45.8	93.1	10.0
7/29	194	0.0	100.0	55.1	86.0	11.3
8/5	178	0.0	100.0	30.3	72.2	2.2
8/12	130	0.0	100.0	34.6	82.2	6.9
8/19	150	0.0	100.0	21.3	67.7	0.0
8/26	378	0.0	100.0	20.9	39.7	1.1
9/2	150	0.0	100.0	15.3	13.0	0.7
9/10	100	0.0	100.0	11.0	10.0	1.0
9/15	100	0.0	100.0	3.0	2.0	1.0

¹ S.a. = *S. acerivorana*

² A.c. = *A. chalybeana*

³ T.a. = *T. asperatella*

⁴ n=Number of rolled leaves examined.

Part II, Table 8. Leaf-roller dominance, mortality and webworm inhabitation in non-disease plots in Florence County, Wisconsin. 1959.

Date	n ⁴	Percent of rolls by		A.c. rolls viable	A.c. population alive	Percent of rolls containing T.a. ³
		S.a. ¹	A.c. ²			
6/27	274	4.7	95.3	78.1	99.0	1.1
7/2	373	1.3	98.7	75.5	99.7	0.3
7/9	353	0.6	99.4	77.2	98.9	3.1
7/16	244	0.8	99.2	59.5	93.7	0.0
7/22	147	1.4	98.6	53.8	97.4	1.4
7/29	394	0.0	100.0	40.6	80.0	0.0
8/5	685	0.0	100.0	35.9	76.8	2.9
8/12	350	0.0	100.0	28.3	71.7	1.1
8/19	307	0.0	100.0	32.6	55.1	1.0
8/26	269	0.0	100.0	23.6	32.0	0.2
9/2	150	0.0	100.0	20.0	33.3	1.0
9/10	200	0.0	100.0	4.5	36.8	1.0
9/15	200	0.0	100.0	7.0	8.3	1.0

¹ S.a. = *S. acerivorana*

² A.c. = *A. chalybeana*

³ T.a. = *T. asperatella*

⁴ n = Number of rolled leaves examined.



Part II, Fig.10. Frass retreat and pupal exuvium of *Acleris chalybeana*.
(Note: normal position of frass retreat is rolled within the skeletonized area to right.)

Most parasitoids attacked the larval stage of the host and emerged either from the larval or pupal stage. The type parasitoid is named for the stage from which it emerged from the host. Twenty-one primary hymenopterous species have been reared from *A. chalybeana* (Table 2); in order of their importance *Oncophanes americanus*, *Scambus hispae*, *Mesochorus* sp. and *Acrolyta* sp. probably *longicornis* comprised 58% of the parasitism. Of the parasitic species recovered, *A. chalybeana* had 11 in common with *S. acerivorana*.

Predators serve to control larval stages and probably are equal in importance to the complex of parasitoids. The percent of viable leaf rolls decreased to the extent that, by September, most collections

resulted in less than 10% of the rolls containing larvae (a figure disproportionate to normal larval abandonment). The most common and important predators were the spiders, *Clubiona* sp., *Xysticus elegans* Keyserling and *Phidippus* sp. The stink bug, *Podisus modestus* (Dallas) (Fig. 11), was abundant in both seasons. A bug, *Deracoris nitenatus* Knight, also was predaceous on roller larvae. Two lacewings, *Chrysopa plorabunda* Fitch and *Chrysopa plorabunda* (Fitch) were inhabitants of rolls and predaceous on *A. chalybeana* larvae as well as on aphids. Leaf-rolling larvae were commonly encountered that were heavily infested with small red mites of the genus *Leptus*.

Gracilaria Species, A Gracilariid Leaf Roller

A lepidopterous skeletonizer of sugar maple, *Gracilaria* sp. probably *packardella* Chamb., previously unrecorded in Wisconsin, has been observed frequently in Florence County. The larvae began their

seasonal development by folding the tip of a lateral lobe and tying the leaf edge securely to the surface, leaving only a small orifice at the apex. Only the lower surface was utilized by this species. The



Part II, Fig. 11. *Podisus modestus* feeding on *Acleris chalybeana* larva.

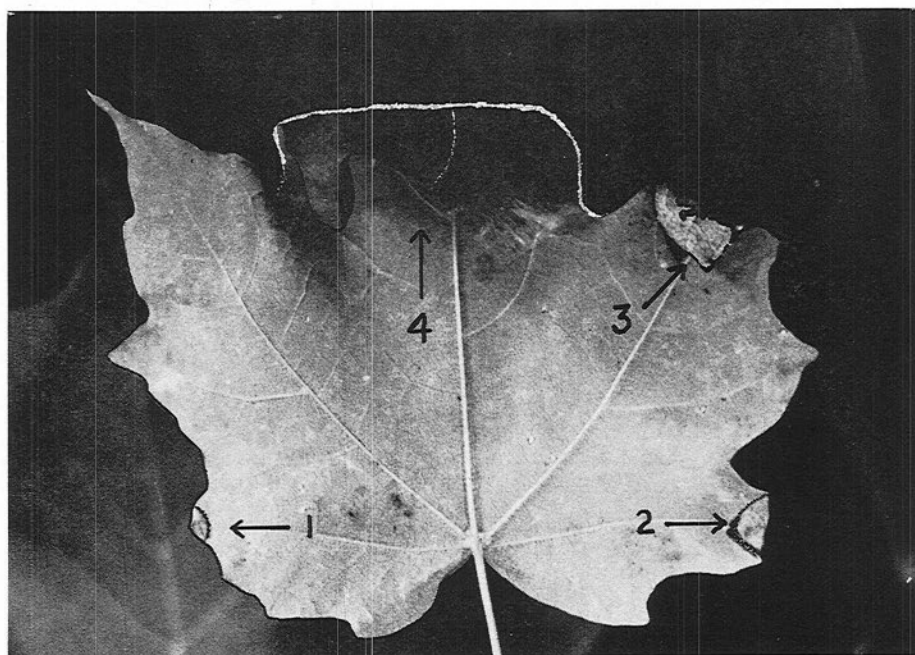
young larva skeletonized the interior of the folded leaf. When the food supply has been exhausted, the larva abandoned the tip-fold and constructed another slightly larger one on a different tip of the same leaf (Fig. 12). This process continued until larval development was complete, and up to five tips of an individual leaf may be folded by the same larva. Frequently, the last tip fold was constructed on the terminal lobe.

When the last larval stage was completed, the caterpillar crawled from the fold interior through the orifice onto the exterior of the folded tip. Here it spun a white, shiny cocoon (Fig. 13); the adult emerged after several weeks. In 1959, pupae were observed by July 4.

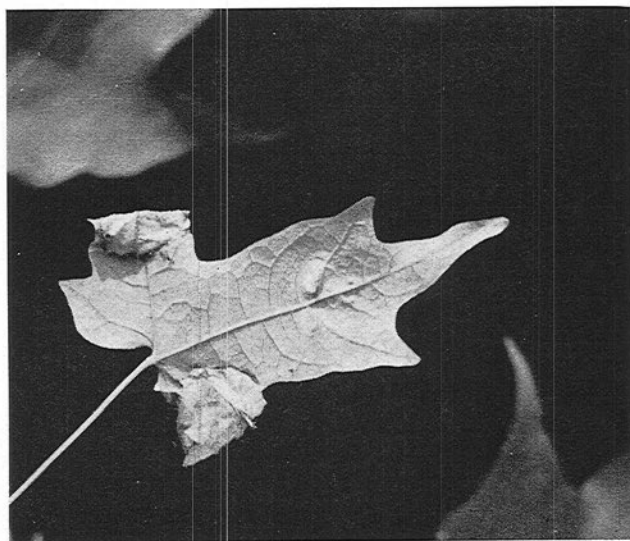
There is no record that this species occurred in high numbers during the leaf roller and webworm epiphytotics of prior

years. However, the deformed leaves were readily used as oviposition sites by the maple webworm. In fact, the leaves were probably the most ideal oviposition sites available to the webworm. Tip-folds were desirable because the degree of folding by this species was fixed; when a fold is constructed, it remains the same size for the life of the leaf. Thus, a fixed area of leaf surface is exposed. This contrasts with *S. acerivorana*, which rolls the leaf completely from the start, and with *A. chalybeana*, whose rolls offer progressively less leaf area as the larvae become more mature.

The following parasitoids were recovered from pupae of this species: *Apanteles ornigis* Weed, *Dicladocerus* sp., *Mesochorus* sp., *Pediobius* sp., *Sympiesis marylandica* Girault and *Sympiesis substigmata* Girault.



Part II, Fig. 12. Progressive tip folding (counterclockwise from bottom left) by *Gracilaria* sp.



Part II, Fig. 13. Pupal exuvium and silken case of *Gracilaria* sp.

The Maple Webworm, *Tetralopha asperatella* (Clemens)

The maple webworm, *Tetralopha asperatella* (Clem.), is an epipaschiine (Pyrilidae) moth found throughout the eastern United States (Craighead, 1950). This species was described by Clemens (1860) as *Lanthaphe asperatella*. Grote (1878) subsequently placed the species in *Tetralopha*. In his major revision of the Epipaschiinae, Hulst (1888, 1889) transferred *asperatella* to *Saluda*; Dyar (1902) listed it under *Benta*. Forbes (1925) recognized *Tetralopha* as valid; Holland and Schaus (1925) and McDunnough (1939) followed this classification.

Distribution

The original specimens were taken in Pennsylvania and Massachusetts (Clemens, 1860); Forbes (1925) reported *T. asperatella* generally distributed throughout New York; Hulst (1889) listed the species from Texas, and Dyar (1902) added the states of Arizona, Colorado and Wisconsin. Felt and Bromley (1941), referring to this species as the elm webworm, found *T. asperatella* commonly in Connecticut. In Canada, the webworm occurs in Ontario (Atwood, 1943), Manitoba and Saskatchewan (Prentice and Hildahl, 1955).

Hosts

The webworm reportedly attacks a variety of hardwood hosts including oak, maple, elm and beech (Forbes, 1925), locust (Hulst, 1889), slippery elm, pin oak, sugar maple (Felt and Bromley, 1941) and poplar (Atwood, 1943). Prentice and Hildahl (1955) reported the first known outbreak of the species on trembling aspen, a condition where 75% of the foliage had been destroyed in some areas. Sugar, red and mountain maple were observed as hosts in Wisconsin.

Life Stages

Egg. The webworm eggs are ovoid, slightly

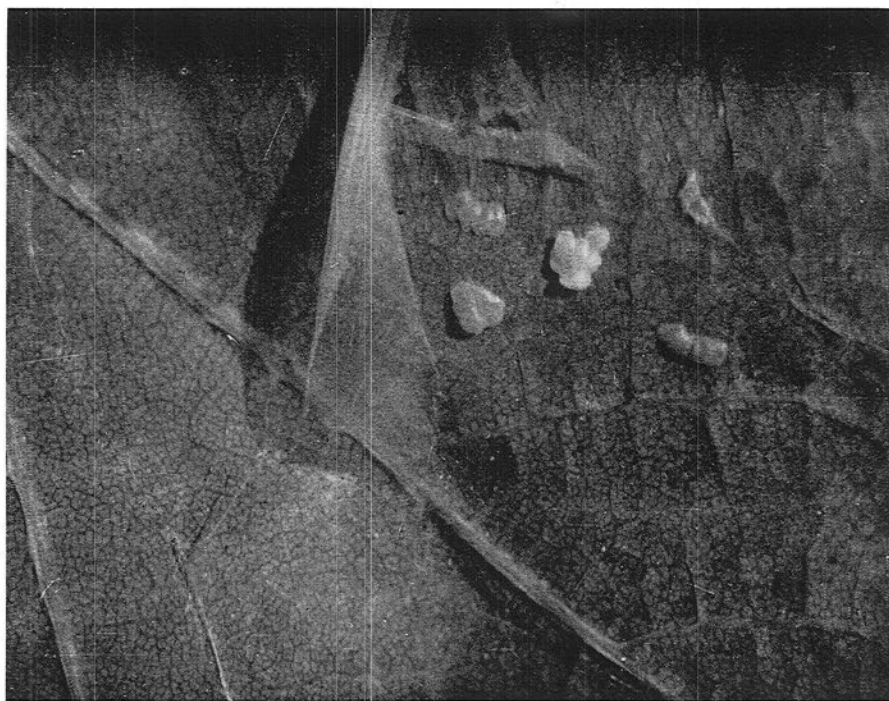
flattened dorsoventrally and creamy yellow when first laid, later they darken to canary yellow (Fig. 14). The reticulous exochorion imparts an iridescent appearance. Blackened eggs were parasitized (Fig. 15). The longest dimension mean is $0.779 \pm 0.065(s)$ mm; width averages $0.551 \pm 0.161(s)$ mm; mean depth is $0.375 \pm 0.035(s)$ mm.

Larvae. The first and last larval instars were well defined, the former by newly hatched individuals and the latter by overwintering forms in the cocoon. A frequency histogram comprised of 1057 samples of preserved larvae collected in 1958 revealed 6 instars (Fig. 16). The calculated head dimensions conform favorably with the actual widths and no instars appear to have been overlooked (Table 9). The same number of larval stages was demonstrated for the pine webworm, *Tetralopha robustella* Zell. (Walliesz and Benjamin, 1960).

Length and color of the larvae vary greatly. Newly hatched webworms have a minimum length of 1.5 mm; mature larvae may attain lengths of 20 mm. The body is mottled and striped. Several color phases occur, ranging from pale yellow through shades of green, to brown and occasionally nearly black. An ultimate stage larva is depicted in Fig. 17.

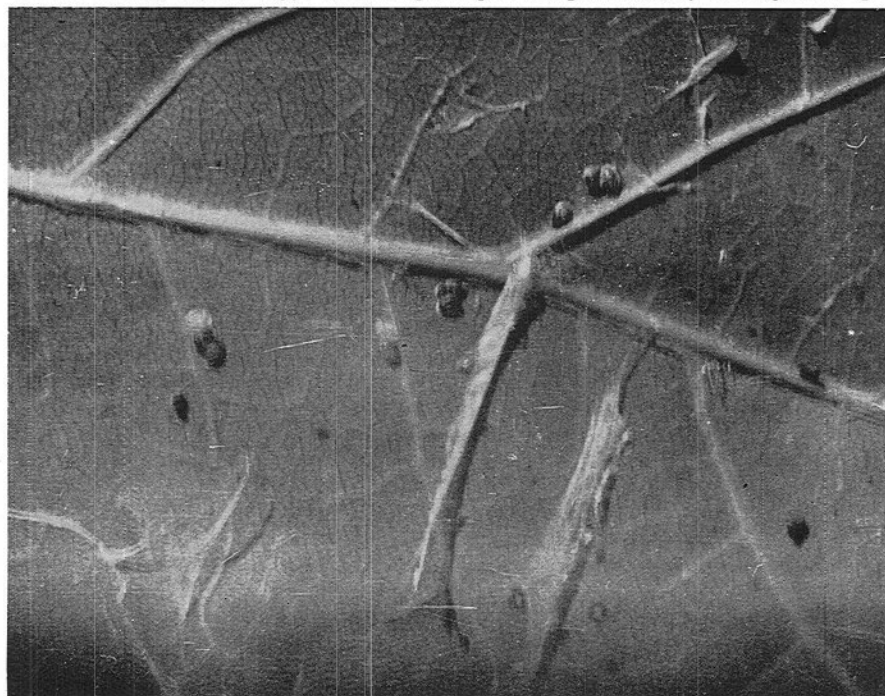
Cocoon. A white silken cocoon, enveloping the overwintering larva and subsequently the pupa, is $9.71 \pm 1.138(s)$ mm in length and $6.33 \pm 1.555(s)$ mm wide.

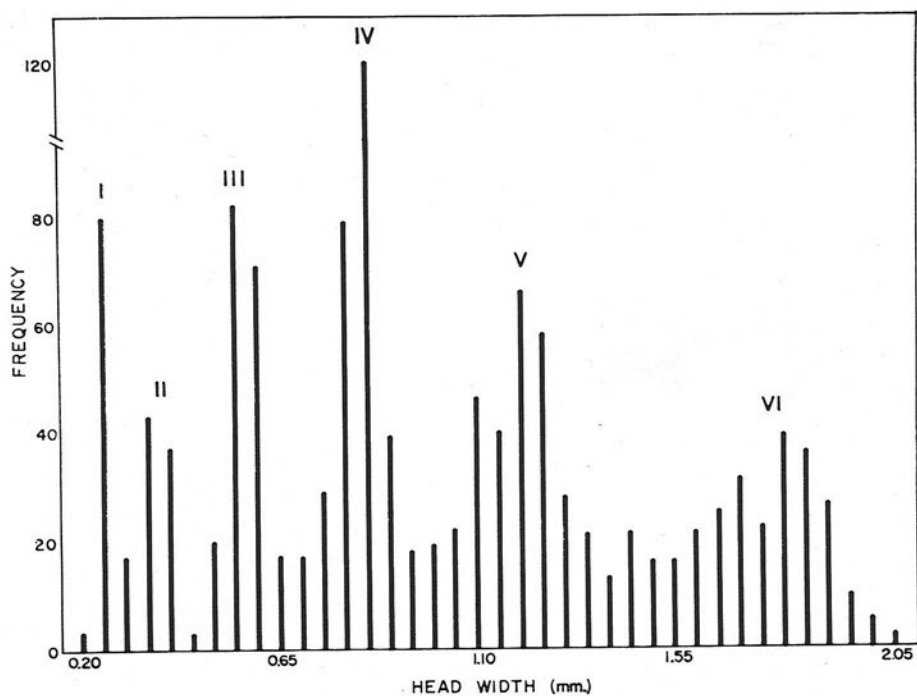
Adult. The body is powdery grey and ranges in length from 20 to 25 mm. The antennal process is longer than the scape, with the plume yellow to black. The outer half of the forewing is somewhat paler than the body. The antemedial tufts are small, but black and contrast well. The antemedial line is double, dark grey, outwardly oblique and, in the male, is interrupted by a translucent cell (Forbes, 1925).



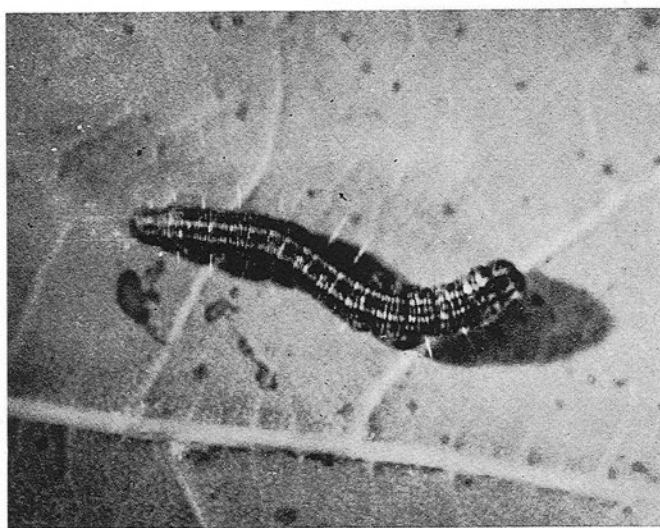
Above: Part II, Fig. 14. Normal eggs of *Tetralopha asperatella*.

Below: Part II, Fig. 15. Eggs of *Tetralopha asperatella* parasitized by *Trichogramma* sp.

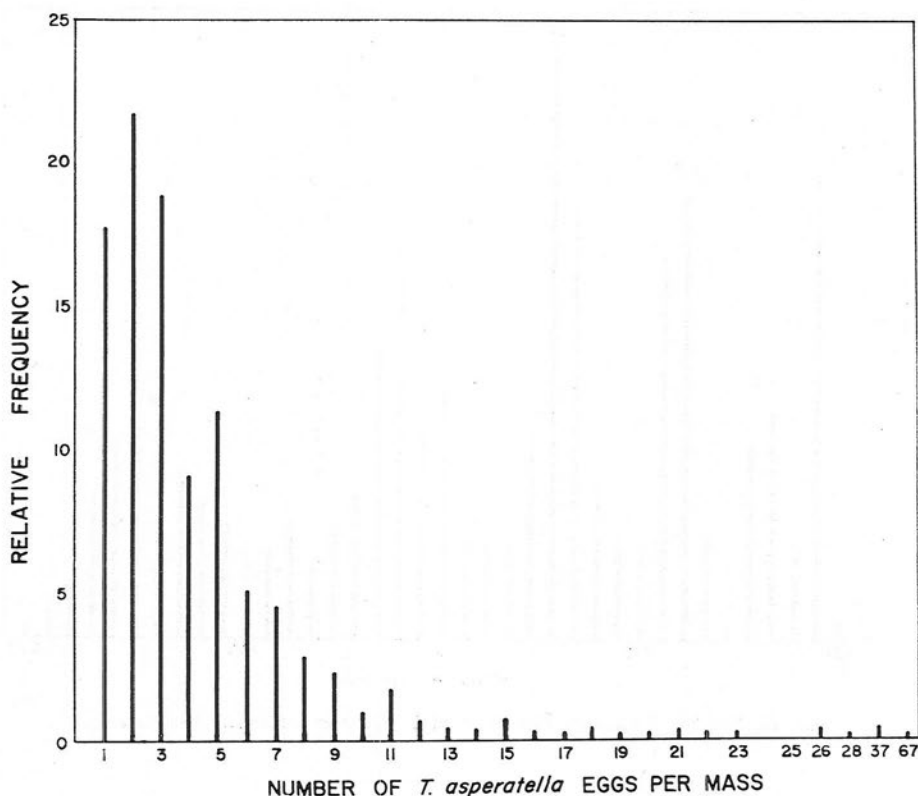




Part II, Fig. 16. Frequency histogram of *Tetralopha asperatella* head-widths.



Part II, Fig. 17. Sixth instar larva of *Tetralopha asperatella*.



Part II, Fig. 18. Frequency histogram of *Tetralopha asperatella* egg masses in 1958.

Life History

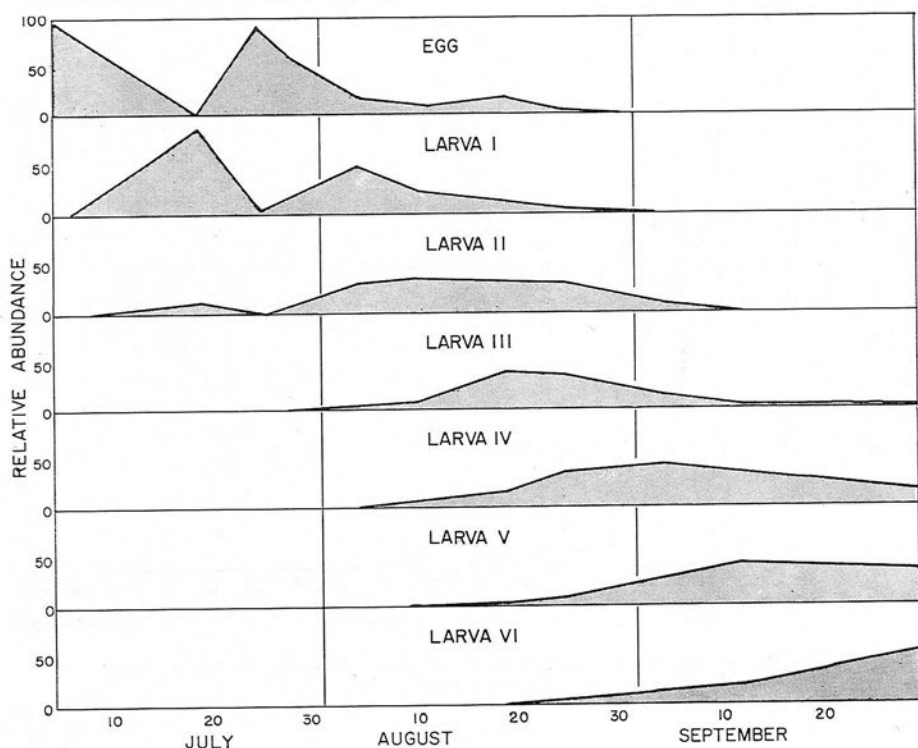
Eggs. Eggs of the webworm were first collected on July 4, 1958; the following year they were present on June 18 throughout Florence County. The mean number of eggs per mass in 1958 was 4.07 ± 0.80 (s) (Fig. 18); the 1959 mean was 3.04 ± 1.89 (s) eggs per mass with a range from 1 to 67 per mass.

The relative abundance of webworm eggs in 1958 was trimodal in distribution (Fig. 19). The major peak occurred in early July, followed in late July by another peak equally as great. In mid-August, a small but measurable increase in the number of eggs took place. In 1958, the oviposition period lasted for 60 days.

Post-oviposition development of the embryos required two to four days. Pre-

paratory to eclosion, the active embryo ruptured the chorion with its mandibles at random on the exposed egg surface.

Oviposition site. Eggs of the webworm were deposited in partially rolled leaves and this association of oviposition in modified leaves was obligatory. In over 5,000 webworm colonies examined, eggs were present only in the leaves rolled by other arthropods. Most commonly, the leaf rolling was caused by *S. acerivorana* and *A. chalybeana*; however, *Gracilaria* sp. and other leaf-rolling Lepidoptera assume a minor role in the provision of oviposition sites. In several instances, eggs were observed in the leaves rolled for spiders' nests. An additional 15,000 leaves, under a range of population densities of these associated insects, were critically examined. These were comprised of groups of three leaves adjacent to a



Part II, Fig. 19. The time distribution of *Tetralopha asperatella* eggs and larvae in 1958.

webworm infested leaf. Inspection for eggs included both surfaces of the leaf blade, the petiole and 4 linear inches of twig to which the leaves were attached. In no instance were webworm eggs observed in other than rolled leaves.

Eggs were found invariably on leaves partially rolled at the time of oviposition. Eggs were most often found in a line, clearly demonstrated to have been the leading edge of the roll as indicated by the position of the silken spans.

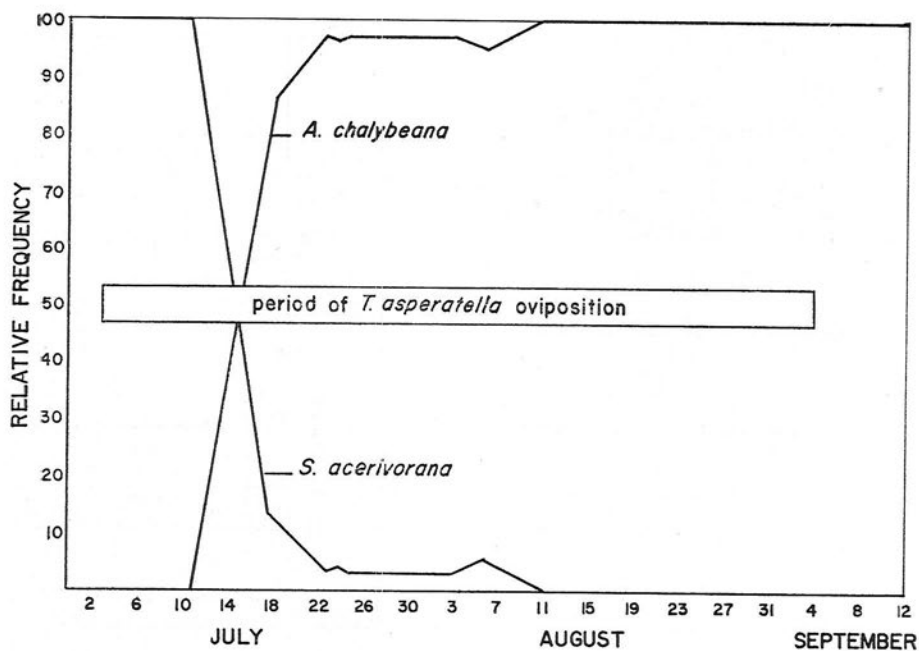
Figure 20 demonstrates webworm oviposition relative to leaf roller abundance and indicates that the leaf roller, *A. chalybeana*, was the most important provider of oviposition sites. Its presence was more concomitant with webworm adults than with the leaf roller, *S. acerivorana*.

Oviposition was induced experimentally by artificially rolling leaves (Giese, 1960), and over 90% of the artificially rolled

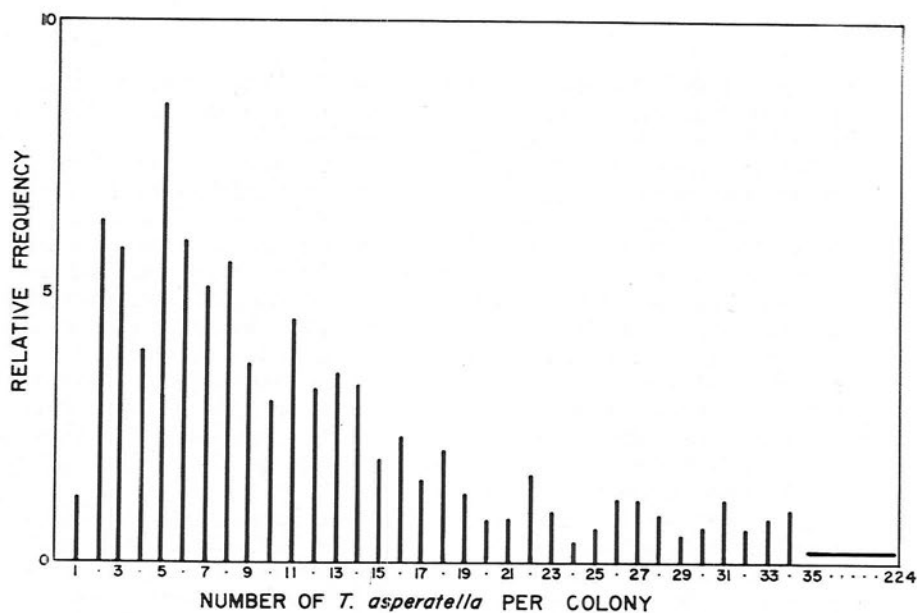
leaves contained one or more of the common leaf roll associates to be discussed under entomosociology.

Larvae. The number of webworms per colony is based on the total number of eggs deposited per leaf. This figure, prior to mortality factors, comprises the theoretical maximum colony size. The mean number of webworms per colony was $18.63 \pm 2.29(s)$ in 1958 (Fig. 21). In 1959, the mean had declined to $8.79 \pm 2.13(s)$; this difference in colony size is highly significant. The maximum colony in 1958 was comprised of 224 individuals; one year later, the maximum colony size was 36.

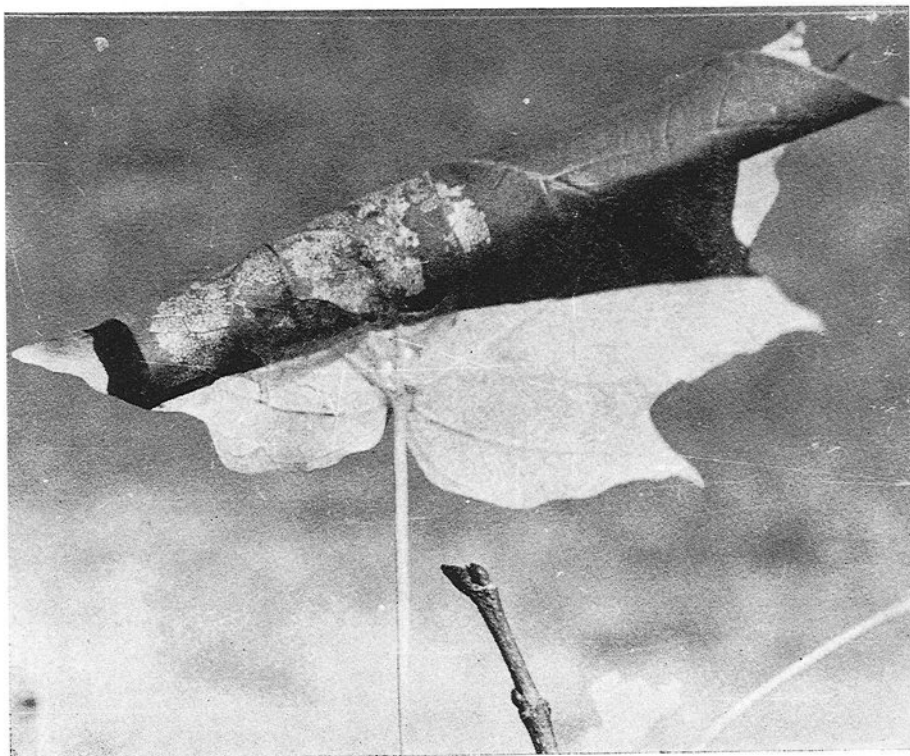
Webworm larvae feed as leaf skeletonizers on the inner surface of the rolled leaf during the first 2 instars. This skeletonization is evident externally (Fig. 22). By the time the major complement of the colony reached the third larval stage, the



Part II, Fig. 20. The oviposition period of *Tetralopha asperatella* related to frequencies in time of 2 leaf rollers in 1958.



Part II, Fig. 21. Frequency histogram of *Tetralopha asperatella* individuals per colony.



Part II, Fig. 22. External evidence of internal skeletonization by early larval *Tetralopha asperatella* feeding in a maple leaf rolled by *Acleris chalybeana*.

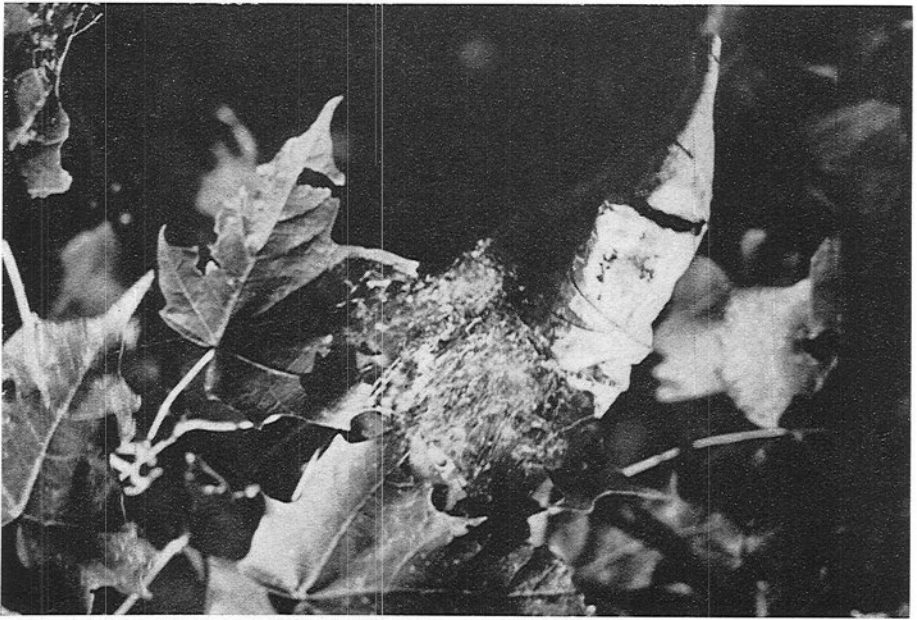
rolled leaf containing the webworms had the leaf structure destroyed and its nutrients exhausted. The larvae then act as true webworms by webbing groups of leaves together. The web is initially comprised of only a few leaves (Fig. 23). In the later stages (Fig. 24), the larvae feed voraciously and great numbers of leaves are included in the web. Toward the end of the feeding period, whole branches are webbed by single colonies.

The time of larval eclosion and web formation is critical in the successful development of the webworm colony. Should the interval between oviposition and the development of the web-forming instars exceed the time required for abscission of the rolled leaf following departure of the roll forming larva, the young webworm colony will fall to the forest floor and die. If, however, the web-forming instars begin feeding prior to abscission

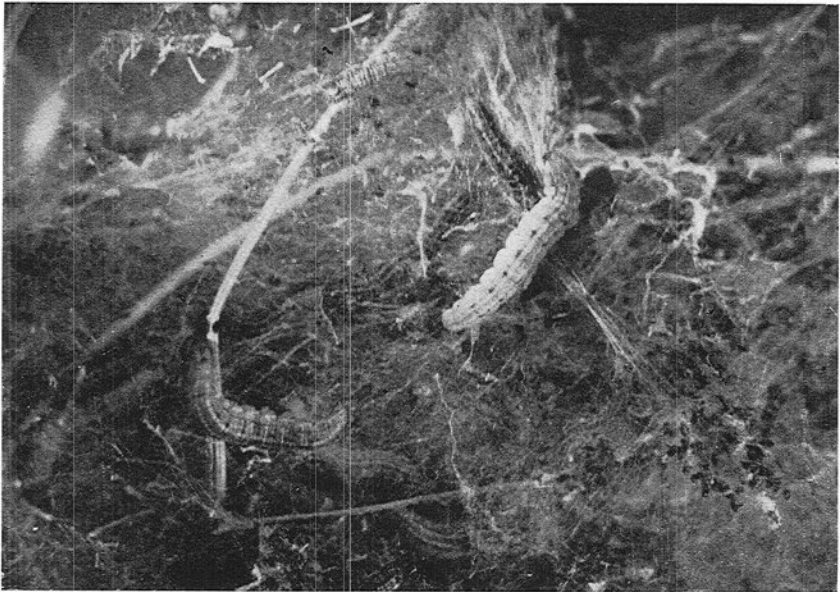
of the damaged leaf roll and the roll is webbed to woody tissue and other leaves, the leaf remains tied to the tree even though the petiole may have subsequently detached. The younger larvae of the colony can then survive.

When webworm infestations are severe, relics of former webs may persist for several years. In the outbreak areas, which coincide with maple blight areas, webworm relics from past years have been observed frequently.

Completion of larval feeding varies with environmental conditions, thus only approximate values may be given for developmental periods of the larvae. The mean period of development for 10 webworms insectary-reared in 1958 from the egg to the prepupa was 3, 4 and 5 days for first, second and third instars, 7 days for the fourth, 10 days for the fifth and



Part II, Fig. 23. *Sparganothus acerivorana* roll (the initial egg niche) incorporated into the web of third and fourth stage *Tetralopha asperatella*.



Part II, Fig. 24. *Tetralopha asperatella* colony comprised of the last three larval stages.

Part II, Table 9. Dimensions of the head and body of the larval stages of
Tetralopha asperatella.

Stage	Number	Actual mean head width (mm)	s	range (mm)	Dyar ¹ ratio	Calculated width (mm)	Number	Actual mean head length (mm)	s	Dyar ratio	Mean body length (mm) ²
L1	100	0.258	0.023	0.20-0.30	—	—	25	0.282	0.024	—	2.35
L2	50	0.373	0.027	0.31-0.44	1.42	0.374	15	0.433	0.036	1.54	4.24
L3	50	0.550	0.039	0.45-0.65	1.53	0.542	25	0.598	0.042	1.38	5.90
L4	50	0.821	0.060	0.66-0.95	1.46	0.786	25	0.854	0.054	1.43	8.35
L5	50	1.190	1.100	0.96-1.35	1.41	1.140	25	1.236	0.111	1.45	12.20
L6	50	1.646	0.143	1.36-2.05	1.45	1.653	25	1.752	0.133	1.42	16.00

¹ Width growth ratio based on 1057 specimens.

² Body length means based on 20 specimens each.

16 days in the sixth instars. The average feeding span was 45 days.

Webworm development was earlier, more rapid and populations were greater in exposed areas than in the dense stands where closure was nearly complete. In the denser, natural stands, though moderate populations were originally present, only a minute fraction ever developed to overwinter. In some instances, the larvae (mainly in the penultimate or younger stages), did not spin cocoons and were subsequently killed by frosts in September and October.

Within a blowdown area in Florence County, 63% of 400 saplings supported a mean of 3.32 webworm colonies per sapling. In 3 adjacent areas, 2 chains from the blowdown, less than 1% of the saplings were infested, and no more than 1 colony per sapling was observed. The development of the larvae was advanced and significantly greater within the blowdown.

Under these open stand conditions: (1) the larvae, within the cocoon, are exposed to more rapid and higher temperature accumulations the following spring and summer, which probably result in earlier adult transformation and oviposition; (2) the larvae are able to complete development prior to killing frosts; and, (3) because of earlier appearance and accelerated growth, the trees are defoliated during the most vulnerable period with respect to growth loss and mortality.

The sixth instar larvae spin to the ground and perigrate to the mineral soil to spin a protective cocoon and overwinter. The cocoon is comprised of silken threads with soil particles and small bits of organic debris incorporated into the structure and are scarcely discernible from the surrounding medium.

Adult. Transformation to the adult occurs from mid-June to early July. In 1958, adults emerged over a 60 day period starting June 3, and 90% of the oviposition was completed by August 15. In

1959, adults were recovered earlier and 90% of the oviposition was completed by August 7. Transformation to the adult took place *en masse* during several periods throughout the season. The egg abundance shown in Fig. 19 infers two major adult peaks; the second of these corresponds to the first peak of light-trapped adults (Table 10).

The sex ratio of adults was 2.13:1 females to males, determined from 266 light-trap collected specimens. This may not be indicative of the true ratio, as a sex differential attraction may exist.

Natural Control

A single unidentified species of *Trichogramma*, a parasitoid of webworm eggs, was recovered from collections made throughout northeastern and northcentral Wisconsin. Under conditions of high host population density, up to 73% egg parasitism was recorded while in enphytotic situations, however, *Trichogramma* adults were rarely observed.

Mesochorus sp. was recovered from webworm larvae. An unknown species of *Cremastus* parasitizes webworm larvae and emerges while its host is a late instar larva and pupates in the web. *Microgaster peroneae* was recovered from larvae. A hyperparasitoid, *Perilampus stygicus* infests *Cremastus* sp.; it prevents its development and emerges as an adult from the white cocoon of its host.

Several species of green and brown lacewings were predaceous on *T. asperatella* larvae; *Chrysopa plorabunda californica*, *Chrysopa plorabunda plorabunda* and *Micromus positicus* have been observed as important predators. The pentatomids, *Meadorus lateralis* and *Podisus modestus* (Fig. 25) were also common predators. Two coccinellids, *Anatis 15-punctata* and *Anatis ocellata* often were associated with the webs of *T. asperatella*; however, their exact role in the complex is not known.

Part II, Table 10. *Tetralopha asperatella* adults taken at ultraviolet traps in 1958.

	Date of collection ¹	Number of adults
July	9	0
	10	0
	12	0
	15	0
	21	0
	22	0
	23	4
	24	263
	27	13
	29	1
	30	7
	31	6
August	4	266
	5	14
	6	71
	7	0
	10	2
	11	551
	13	36
	14	9
	15	7
	16	0
	29	0

¹ All collection dates represent the operation of a single trap except for July 12 and August 11 when three traps were operated in three different stands. The catch on August 11 was 101, 201 and 249 for the three traps.

The Entomosociology of the Sugar Maple Insect Complex

A complex ecological relationship exists between the lepidopterous defoliators previously discussed and their arthropod associates in the rolled leaves. The study of these insect communities and their relationship to one another is hereby termed *entomosociology*. The absolute dependence of *T. asperatella* on three species of leaf rollers is of paramount importance in the development of ephipyotics of this species.

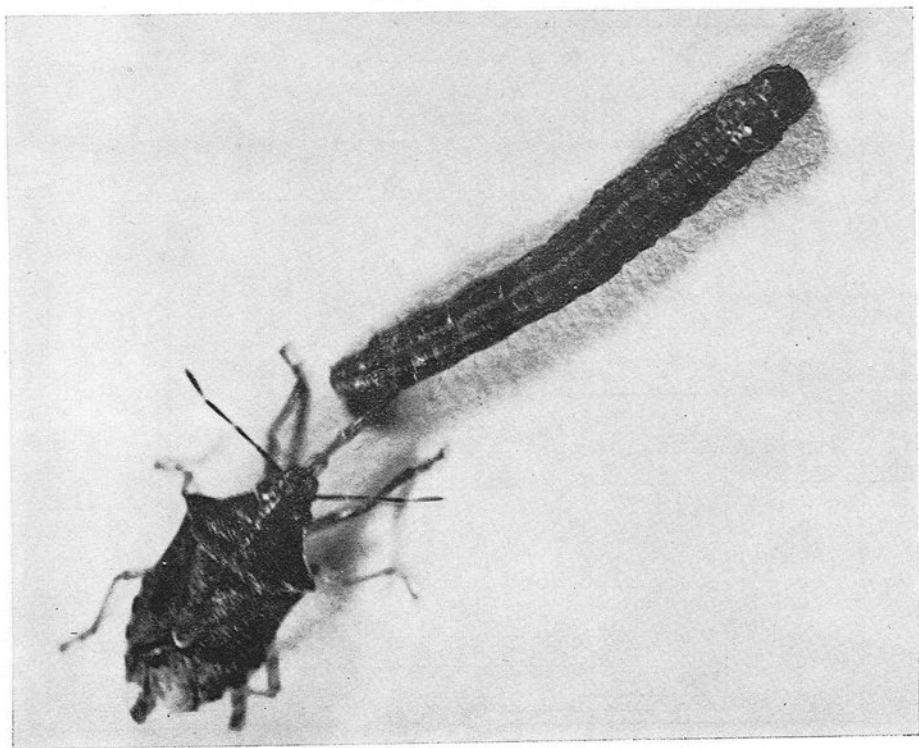
The rolled-leaf habitat is attractive to a number of arthropods (Table 11), and

several insect species complete their entire life development within the rolled leaves. The arthropod complex associated with this microhabitat thus is a community unto itself (Figure 26).

In over 500 aphid colonies examined in 1958 and 1959, all but one occurred in the rolled leaves. These aphids apparently attain maximum development in rolled leaves. The percentage of rolls infested with aphid colonies in 1958 was significantly less in diseased areas than in non-diseased areas (Table 6).

Part II, Table 11. Arthropod associates included in the rolled-leaf insect communities of northeastern Wisconsin.

Associate	<i>S. acerivorana</i>	<i>A. chalybeana</i>	<i>T. asperatella</i>
Psocoptera: Polypsocidae			
<i>Polypsocus curruptus</i> (Htg.)		*	
<i>Anomopsocus amabilis</i> (Wish.)	*		
Hemiptera			
Miridae			
<i>Deracocaris nitenatus</i> Knight	*	*	
Pentatomidae			
<i>Podisus modestus</i> (Dallas)		*	*
<i>Podisus placidus</i> Uhler	*		
Homoptera: Aphidae			
<i>Drepanaphis</i> sp.	*	*	
Neuroptera			
Chrysopidae			
<i>Chrysopidae p. plorabunda</i> Fitch		*	*
Hemerobiidae			
<i>Hemerobius humulinus</i> L.		*	
Coleoptera			
Coccinellidae			
<i>Anatis 15-punctata</i> (DeG.)		*	*
<i>Anatis ocellata</i> (L.)	*	*	*
<i>Anisocalvia 12-maculata</i> (Geb.)		*	
<i>Anisocalvia 14-guttata</i> (L.)		*	
<i>Hyperas bigeminata</i> (Rand.)		*	
Lathridiidae			
<i>Melanophthalma pumila</i> Leb.	*	*	*
Staphylinidae	*	*	
Lepidoptera			
prob. <i>Recurvaria</i> sp.		*	*
<i>Acleris chalybeana</i> (Fern.)	*		
<i>Tetralopha asperatella</i> (Chem.)	*	*	
<i>Gracilaria</i> sp.			*
Arachnida			
<i>Clubiona</i> sp.	*	*	*
<i>Xysticus elegans</i> (Keys)	*	*	*
<i>Phidippus</i> sp.	*	*	*



Part II, Fig. 25. *Podisus modestus* attacking a *T. asperatella* larva.

The presence of aphids encourages aphid predators, and probably explains the frequency with which coccinellid larvae and adults occurred. Though rolled leaves commonly contain these beetles, only 1 beetle was present in a roll.

Green and brown lacewings also were probably attracted to the aphids, but leaf roller larvae and larvae and eggs of the webworm were acceptable hosts also. Conversely, mites of the genus *Leptus*, which were common on living larvae of leaf rollers and webworms, find suitable hosts in aphids and lacewings.

A predaceous plant bug was a primary predator of aphids. However, later in the season when webworm oviposition occurs in the rolled leaves, the bug destroyed large numbers of webworm eggs.

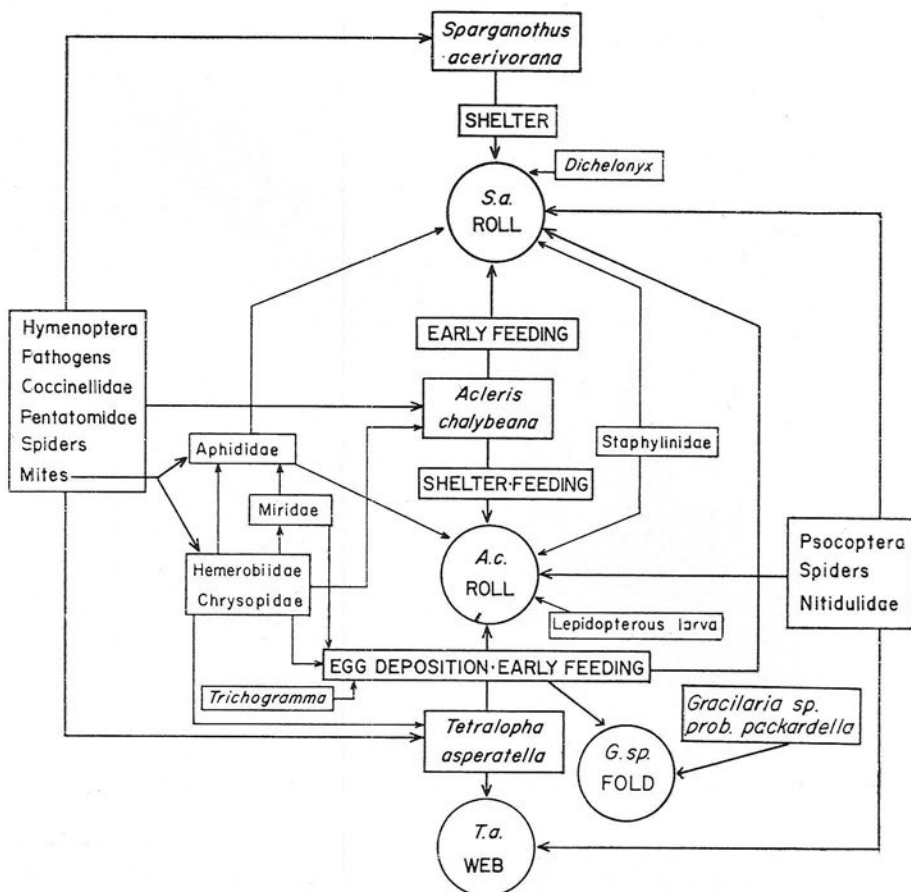
Of the pentatomid predators, *Podisus modestus* outnumbered the others in the order by 14 times. Eggs were deposited in the rolled leaf, or less commonly the insect entered from outside of the roll.

The nymphs then fed on the leaf-rolling hosts and were supplied more hosts when webworms ultimately dominated the rolls.

Two species of bark lice (Psocoptera) complete their development in rolled leaves. *Anomopsocus amabilis* was found exclusively in rolls, and *Polypsocus corruptus* rarely was found on exposed leaves early in the season.

Stink bugs, lady bird beetles, green and brown lacewings, sciarids and numerous spider species were able to complete their life cycle in rolled leaves; however, the same species are known from other habitats as well. Sciarid larvae occasionally were recorded; immature members of this family feed on fungi.

Seven species of lepidopterous larvae have been collected from rolls. One, an undetermined Gelechiid, has been recovered from sugar maple only in rolled leaves. The remainder most frequently occur as independent defoliators. As their presence probably resulted from the chance ovi-



Part II, Fig. 26. The entomosociology of a sugar maple leaf roller-webworm complex.

position on leaves which later become rolled, they are not considered an integral part of the rolled-leaf insect community.

Usually 2 or 3 staphylinids, but as many as 6, were found in each of the leaf rolls and webs and they persisted throughout the season. The percentage of leaves having rove beetles was over 7 times greater in diseased (open) stands than under the more vigorous closed stand conditions (Table 6).

The most noticeable forms to frequent the rolls were the spiders. They utilize the leaves for nesting and egg laying sites, and are predators of the leaf-

rolling and web-forming insects also. The precise role that the bark lice fulfill in the community is not known. As a group, they generally are feeders on fungi and dead insects. Lathridiids are minute, brown, scavenger beetles usually associated with animal or vegetable debris.

The fidelity of association also is confirmed by parasitoids and predators which are frequently common to 2 of the leaf rolling hosts or 1 of the leaf-rollers and the webworm (Table 2). All 3 of aforementioned defoliators were hosts of the primary larval parasitoid, *Microgaster peroneae*.

General Invertebrates Associated with Sugar Maple

Sugar maple is attacked by great numbers of lower animals besides the leaf-rollers and webworm discussed previously. In general, a paucity of knowledge exists concerning insects affecting the upland northern hardwoods. To increase the knowledge on lower animal fauna associated with sugar maple a preliminary faunistic survey was conducted in and adjacent to the blight area; the fauna examined are reported here.

Defoliating Insects

In addition to the forms discussed elsewhere, seventeen species of general defoliators were collected (Table 12). The most common members of the defoliating group in 1958 and 1959 were the trumpet skeletonizer, *Epinotia aceriella* and the scarabid, *Dichelonyx* sp.

Seed Insects

A collection of 1,810 seeds from the fall seed crop on sugar maple in Florence County were 1.93% parasitized. The remainder of seeds from which parasites had not emerged were placed in capsules. No additional insects were recovered, indicating primary infestation when the seeds are still on the tree.

Gall Forming Insects and Mites

The maple spindle gall caused by the mite, *Phyllocoptes aceriscrumena* Riley, was the most abundant of the tissue-deforming organisms in 1958 and 1959. An undescribed species of Cecidomyiidae and hitherto unrecorded type of leaf damage also were discovered. The leaves were severely distorted; all damaged leaves thus far examined were of sucker sprout origin and were produced at a later date than the normal foliage. Gall midges, *Cecidomyia ocellatus* O.S. and *Dasyneura communis* Felt., attacking sugar maple were commonly encountered.

Part II, Table 12.

A list of defoliating insects of sugar maple in Florence County, Wisconsin. 1958-1959.

Lepidoptera

Arctiidae

Halisidota spp.

Gracilariidae

Lithocolletis aceriella (Chem.)

Lithocolletis lucidiocostella (Chem.)

Gracilaria sp. prob. *packardella*

Incurvariidae

Paraclemensia acerifoliella Fitch

Lasiocampidae

Malacosoma disstria Fab.

Lymantriidae

Dasychira sp.

Noctuidae

Acronicta americana (Harr.)

Lithophane bethunei G. & R.

Notodontidae

Heterocampa guttivitta (Wlkr.)

Olethreutidae

Epinotia aceriella (Chem.)

Pyrilidae

Tetralopha asperatella (Chem.)

Saturniidae

Callosamia polyphemus (Cram.)

Hyalophora cecropia (Linn.)

Tortricidae

Sparganothus acerivorana MacKay

Acleris chalybeana (Fern.)

Coleoptera

Crysomelidae

Bassareus sp.

Donacia sp.

Synata sp.

Scarabaeidae

Dichelonyx sp.

Part II, Table 13. Insects associated with the woody tissue of non-vigorous sugar maple in Florence County, Wisconsin. 1958-1959.

Lepidoptera

Aegeriidae

Sylvora acerni (Chem.)

Coleoptera

Buprestidae

Agrilus sp. (prob. *masculinus* Horn.)

Dicerca sp. (prob. *divaricata* Say)

Cerambycidae

Anoplodera proxima Say

Anoplodera vittata Swed.

Glycobius speciosus Say

Cucujidae

Cucujus clavipes F.

Endomychidae

Endomychus biguttatus Say

Erotylidae

Tritomen sp.

Eucnemidae

Dirbagus sp.

Pyrochroidae

Dendroides canadensis L.

Hymenoptera

Formicidae

Lasius alienus Prov.

Xiphydriidae

Xiphydria albicornis Harr.

Sucking Insects

Six sucking forms were collected, including the aphid *Drepanaphis* sp. (generally found within the rolled leaves) and two cicadellids, *scapholdeus* sp. and *Graphocaphala coccinea* (Forster). The most common homopterans were scales, *Pulvinaria innumerabills* (Ruthr.), *Lecanium corni* Bouche and *Lecanium* sp. prob. *quercifey* Fitch. One unidentified Membracid was taken.

Insects Associated with the Woody Tissue of Non-vigorous Trees

The decline of sugar maple caused by

maple blight resulted in the invasion of dead and declined-vigor trees by secondary insects and pathogens. The sugar maple borers, *Glycobius speciosus* and *Xiphydria albicornis* were common (Table 13). Staining by ambrosia beetles and their associated fungi was frequently found, but the beetles were not recovered.

Non-arthropod Pests

Two injurious snails, *Allogona profunda* Say and *Stenotrema fraternum cava* Pilsbry, and *Vanatta* occasionally were found in Florence County.

Summary

Sugar maple stands in which maple blight occurred had been severely defoliated by two leaf rollers and the maple webworm. The close spatial and time coincidence of this defoliation and the appearance of maple blight strongly suggested that these insects were involved with the development of the disease.

The leaf roller, *Sparganothus acerivorana*, a new record for Wisconsin, was the initial defoliator in the complex of primary insects attacking sugar maple to appear in the year. Solitary larvae began rolling the lower surface of leaves in early June and included the entire leaf in their rolls. The rolled leaf served as a retreat and pupal chamber; feeding occurred on adjacent leaves. Sugar maple was the main host; red, silver and mountain maple also were fed upon. Basswood, ironwood, yellow birch and American elm were accepted when presented to the larvae.

Of the 20 primary parasitic Hymenoptera reared from this leaf roller, *Apanteles polychrosides*, *Mesochorus sylvorum*, *Meteorus trachynotus*, *Microgaster epagoges* and *Phaeogenes* sp. (in order of importance) comprised more than 83% of all parasitoids. Other natural control agents included spiders *Clubonia* sp. and *Xysticus elegans*, and the pentatomid *Podisus placidus*. Leaf roller populations were reduced to the general equilibrium position, by parasitism, predation and adverse weather conditions in 1958 and 1959.

The leaf roller, *Acleris chalybeana*, also a new record for Wisconsin, was the second species in the sugar maple defoliator sequence to appear. Larvae of this solitary species rolled only the lower leaf surface from early to mid June through July, and preferred the lateral main lobes. The host list included sugar, red, and mountain maple, ironwood and yellow birch. Larvae fed on the rolled leaf until it was destroyed, then attached themselves to adjacent new leaves where they continued to feed. Pupation took place within a frass chamber in a rolled leaf in August. Overwintering is in the larval stage.

A comparison of leaf rolling by this species, *S. acerivorana*, and *Gracilaria* sp. is presented.

The magnitude of leaf roller population, as measured by the number of leaf rolls, was greatest in diseased stands; in areas where blight did not occur the leaf roller population was from 1/3 to 1/8 as great.

Natural control factors associated with this leaf roller include 21 Hymenoptera among which the following were of most importance: *Oocophanes americanus*, *Scambus hispae*, *Mesochorus* sp. and *Acrolyta* sp. probably *longicornis*. Eleven of the 21 parasitoids were also reared from *S. acerivorana*.

Most common among the predators were the spiders *Clubonia* sp., *Xysticus elegans*, and *Phidippus* sp. and the stink bug, *Podisus modestus*.

A third leaf roller, *Gracilaria* sp. probably *packardella*, also a new record for Wisconsin, rolled the leaves of sugar maple. Larvae folded the lateral tips of leaves and skeletonized their interior. When the food supply was exhausted they moved to another tip on the same leaf and folded it; up to 5 tips of an individual leaf might be folded by a single larva. Pupation took place on the exterior of the last folded tip. There were no records of high populations of this roller during the leaf roller-webworm outbreaks. Several parasitoids were reared from pupae of this leaf roller.

The maple webworm, *Tetralopha asperatella*, attacked a variety of hardwoods including sugar, red and mountain maple in Wisconsin, and oak, beech, elm, locust and aspen elsewhere in North America.

This species caused severe defoliation of sugar maple in the area where blight was later discovered.

Eggs of the webworm are laid on the surface at the edge of the roll on partially rolled leaves. This is an obligatory phenomenon; in over 5000 webworm colonies examined, eggs were present only in leaves rolled by other arthropods. No webworm eggs were observed on 15,000 non-rolled leaves adjacent to webworm

colonies. Oviposition began in mid June and continued into mid August with 3 peaks occurring in early July, late July and mid August. *A. chalybeana* provided most of the oviposition sites.

Larval feeding is colonial; in 1958 the mean number of larvae per colony was 18.6 and in 1959 it was 8.8. Webworms fed as skeletonizers during the first 2 instars on the rolled leaf; in the third and subsequent instars they webbed adjacent leaves together. Toward the end of their feeding period entire branches were webbed together by single colonies. Feeding began in early July and reached its peak with maximum leaf destruction in mid August to mid September. Overwintering was in the sixth larval stage in a cocoon. Oviposition and adult transformation occurred in mid June to early July.

Natural control factors associated with

the webworm include the following:

1. An egg parasite *Trichogramma* sp. that destroyed up to 73% of the egg.
2. *Mesochorus* sp., *Cremastus* and *Microgaster peroneae* on the larvae.
3. Predatory lacewings *Chrysopa plorabunda californica*, *C. p. plorabunda* and *Micromus positicus*.
4. Predatory bugs *Meadorus lateralis* and *Podisus modestus*.

The entomosociology of the rolled maple leaf and its inhabitants is discussed. Of paramount importance is the absolute dependence of *T. asperatella* on the leaf rollers that predispose leaves to oviposition. The fidelity of the association in the rolled leaves is confirmed by the parasitoids and predators that frequently are common to the 2 leaf rollers and to the webworm.

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PART III.

Pathogens Associated with Maple Blight

David R. Houston¹ and J. E. Kuntz²

Introduction

MAPLE BLIGHT APPEARED unlike previously reported diseases of sugar maple. It differed also from maple dieback (Kuntz and Shea, 1956) reported elsewhere on older maples, in that maple blight developed rapidly and involved trees regardless of age and size (Houston 1961). Maple blight occurred in managed stands with a history of selective logging. These stands had been severely defoliated by insects (2 leaf rollers, *Sparganothis acerivorana* MacKay and *Acleris chalybeana* (Fernald); and the maple webworm, *Tetralopha asperatella* (Clemens) (Giese, 1960)) one or more times during the period from 1955 through 1957.

At that time insects were discounted as a primary cause of maple blight largely because there was no precedent for such damage to sugar maple by defoliation, even though many insect defoliators of sugar maple have been reported (Craighead, 1949; Godman, 1957).

The purposes of this study were (1) to determine the role of possible disease incitants, (2) to clarify the symptomatology and the rate and manner of disease development in individual trees and within stands, and (3) to determine the effects of environmental factors upon disease development.

Methods and Materials

Stands

Trees used in these particular studies were growing in well-stocked, northern hardwood forest stands in Florence County in northeastern Wisconsin. These stands, characteristically with trees of mixed ages and sizes, were composed

principally of sugar maple with a good admixture of eastern hemlock, *Tsuga canadensis* (L.) Carr., yellow birch, *Betula alleghaniensis* Britton, basswood, *Tilia americana* L., ironwood, *Ostrya virginiana* (Mill.) K. Koch, and American elm, *Ulmus americana* L. The forest areas had been under sustained yield management

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for over 30 years, and had received from 1 to 3 selective harvest cuts. Detailed descriptions of similar stands are given in Part I.

Disease Development

Seasonal symptom development was measured during 1958 with biweekly examinations of diseased trees. In addition, photographs of selected trees exhibiting various stages of decline were taken weekly in 1958, biweekly in 1959, and monthly in 1960. Disease development was studied within stands and within individual trees. Permanent study plots, 0.2-1.6 acres in size, were established both in severely blighted and in non-blighted areas. The trees and saplings on these and other special plots were numbered and their positions mapped exactly with a plane table, tape or range finder, and alidade. Visual estimates of the percentage of the crowns affected by maple blight were made for each tree at the start and close of each growing season. In some cases, the junction of live and dead tissue on stems and branches was marked with paint so that progression of symptoms could be detected.

The years were determined in which maple blight had developed in 4 major blight areas (Fig. 1). Fifty terminal branches which showed dieback were collected from saplings in each of the blighted areas. The year that each branch had died was determined by comparing the number of growth rings of the dead (distal) and of adjacent living (proximal) tissue. A saturated solution of phloroglucinol in 18% hydrochloric acid was used as a stain to differentiate the growth rings.

Ecological Factors

Measurements of the compositions and densities of blighted and non-blighted stands were made by the quarter method of Cottam and Curtis (1956). In each stand, 40 points were located at 2-chain intervals along parallel compass lines placed 2 chains apart so as to cover the stand. The space at each point was di-

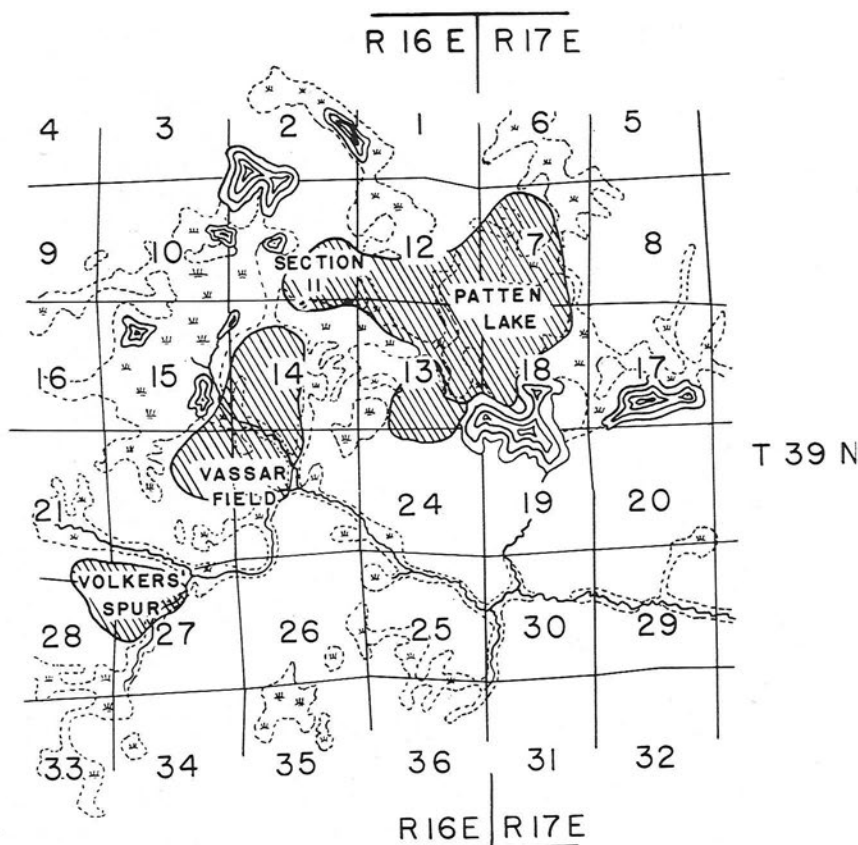
vided into 4 equal quarters with the compass line as 1 bisect. The nearest living tree and sapling within each quarter were located and their species, distances from the point, basal areas, and disease conditions were recorded. At the same time the diseased stands were reconstructed as they existed prior to maple blight. For this, a second set of measurements, made at each point, included dead trees and saplings as well as stumps of trees cut for salvage if these were nearer to the points than were the living trees and saplings. The basal areas of the stumps were recorded. From the data were calculated the frequencies, densities, and dominances (basal area) (Curtis, 1956). The importance values (sums of relative frequencies, densities, and dominances) and continuum indices (importance values x adaptation values) then were computed for each species and stand (Brown and Curtis, 1952). The 2 sets of data were compared and the effects of maple blight were determined on the species composition, density per acre, and the basal area per acre.

Stumps of blighted trees cut for salvage several months to a year previously, and stumps of nonblighted trees cut at the same time were examined for the presence of possible pathogens, especially *Armillaria mellea* (Vahl.) Quel. The severity of attack by this fungus was calculated as the percentage of the root collar circumference covered by fungus rhizomorphs or mycelial fans.

Isolations and Inoculations

Isolations were made of fungi and bacteria from tissues of affected trees. Acidified and nonacidified 2% potato-dextrose and malt agars served as the culture media. Isolates were grouped according to their gross cultural characteristics and representative ones were used in inoculation trials.

Inoculation experiments employed healthy maple saplings, 0.5-4.0 inches dbh and 8-30 feet tall, located in the understory of dense stands, 1-7 miles from the nearest blighted stand. The in-



Part III, Fig. 1. The 4 areas examined in disease development studies. The cross-hatching delineates areas of heavy tree and sapling mortality determined by an aerial survey in 1957. (Aerial survey charts redrafted from the original by permission of the Wisconsin Conservation Department.)

oculum, consisting of bits of diseased host tissue or fungus mycelium of isolates grown on agar or on whole wheat-oat grain medium, was introduced in variously placed knife cuts made through the bark of lateral roots, stems, and branches. Bacterial cell suspensions were sprayed into similar fresh wounds and onto leaves punctured repeatedly with pins. Such leaves were water-soaked prior to inoculation by placing them between wet paper toweling for several hours. In most cases, the inoculated wounds were covered with either dry or moist cotton held by adhesive masking tape. In some cases, the saplings were defoliated manually prior to or following inoculation.

Transmission of possible viruses was attempted. Ten 4-mm disks of leaf tissue from diseased trees were mascerated in 1 ml of a 0.3 M phosphate buffer at pH 8. This mascerate was rubbed onto the leaves of potted 1-year-old maple seedlings and onto leaves or cotyledons of a series of herbaceous virus indicator host plants. Leaves were dusted with carborundum abrasive (Mesh #600) prior to inoculation. In other trials, bark patches cut from diseased trees with a cork borer replaced bark patches removed from healthy saplings. The patches on the inoculated saplings were held in place with masking tape wrapped tightly around the stems.

Plant parasitic nematodes associated with deteriorating maple stands were collected and identified (Riffle, 1962). The pathogenicity of certain species on maple and other tree roots was demonstrated (Riffle, 1963).

Defoliations

Maple saplings growing in the open and in the understory of dense stands were defoliated manually to simulate natural insect defoliation. Saplings were bent over carefully, and the leaf blade tissues were stripped off by hand. Usually, the leaf ribs and petioles adhered to the twigs until abscission occurred about 1 week after treatment. All branches and buds that had died previously also were removed both from defoliated saplings and from paired, nondefoliated, control saplings to insure that all subsequent bud

and twig mortality developed after treatment. At weekly or biweekly intervals during a season different groups of 10-20 saplings each were defoliated once completely. A few groups were defoliated twice in the same year. In other experiments, the leaves were removed from selected branches only.

The effects of defoliation upon the saplings were measured during the season of treatment and in subsequent years. Crown damage was expressed as the percentage of live and dead terminal bud-groups (terminal bud plus its internode of at least 0.5 inch) on all or a part of the upper crown. The pattern of subsequent sapling mortality was recorded and was related to the presence of nearby dead trees or stumps. Local moisture and temperature conditions in the defoliation plots were measured with hygrothermographs placed in shelters 18 inches above the ground near the plot centers.

Observations and Experimental Results

Symptomatology of Diseased Trees

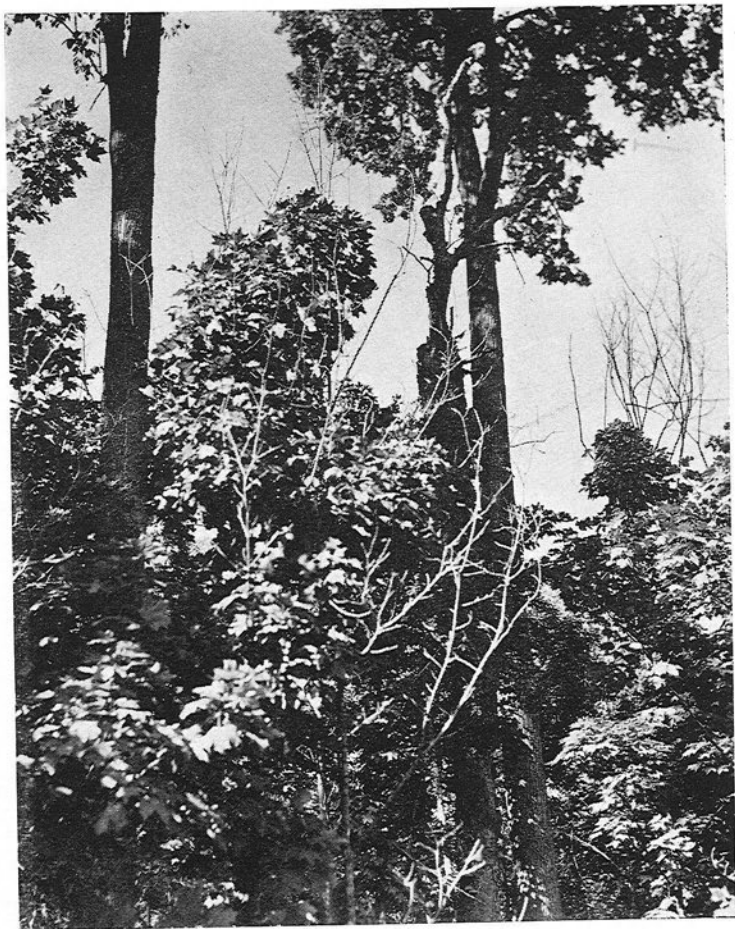
Symptoms of the disease were limited to sugar maple. Trees in all stages of decline were present in the blighted stands. Some trees showed only one to several dead branches; many had diseased branches scattered over the entire crown; others sustained only a few live sprouts near the ground line; many were dead. On the living trees, affected branches often bore a few, scattered, small, slightly chlorotic leaves in the spring and early summer. By midsummer, the majority of these leaves had become increasingly chlorotic, wilted, and brown. Eventually these leaves dropped off. The susceptibility of branches to damage was not influenced by their location on the tree. Within individual branches, however, the smaller, distal portions suffered most damage. Frequently, one to several years' growth was killed back on branches scattered over the entire tree crown. Dead terminals projected beyond the remaining foliage (Fig. 2). Nearly every tree developed epicormic

sprouts (Fig. 3). These sprouts arose primarily from latent buds at the base of dead portions of branches, and on the boles of the trees. The entire foliage of many trees was of epicormic origin and gave a "tufted" or "bunchy" appearance to the crown. (Fig. 4).

In Diseased Stands

Maple blight areas were poorly defined. No sharp boundaries, but rather gradual transitions existed between diseased and apparently healthy stands. Within diseased stands, however, there were local areas of severe damage where "pockets" of dead trees occurred. Dead trees also were scattered throughout the stands.

Severely blighted stands differed greatly in appearance from unaffected stands. In many blighted stands, mortality of saplings and pole-sized trees, along with salvage of dead and dying saw timber trees, opened the stands (Fig. 5). Where the opening was severe, a considerable lush ingrowth of raspberries



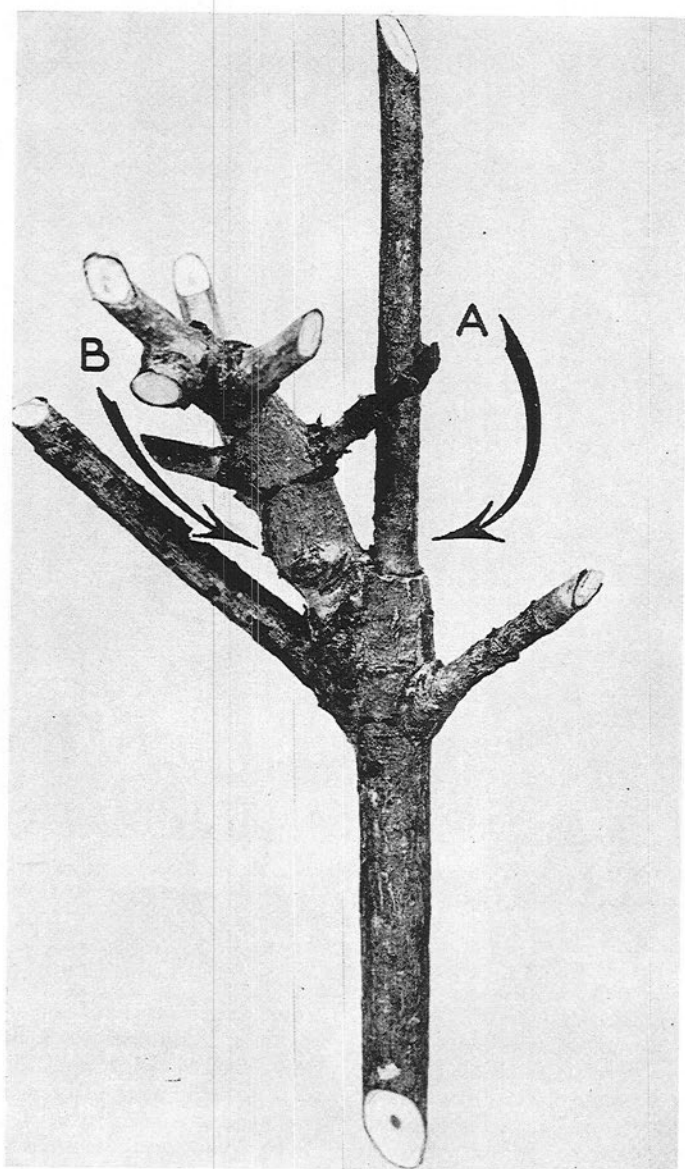
Part III, Fig. 2. Terminal dieback symptoms on branches of naturally defoliated saplings. Dead branches protrude beyond the copious foliage of epicormic sprouts.

(*Rubus* sp.), nettles (*Urtica gracillis* Ait.), and various grasses and broad-leaved weeds developed (Riffle, 1962). Most of the common ground cover layer plants normally found in a dense maple woods were either absent or sparse. A detailed description of the understory composition is presented in Part I.

Disease Development within Individual Trees

The development of maple blight symptoms within individual trees was

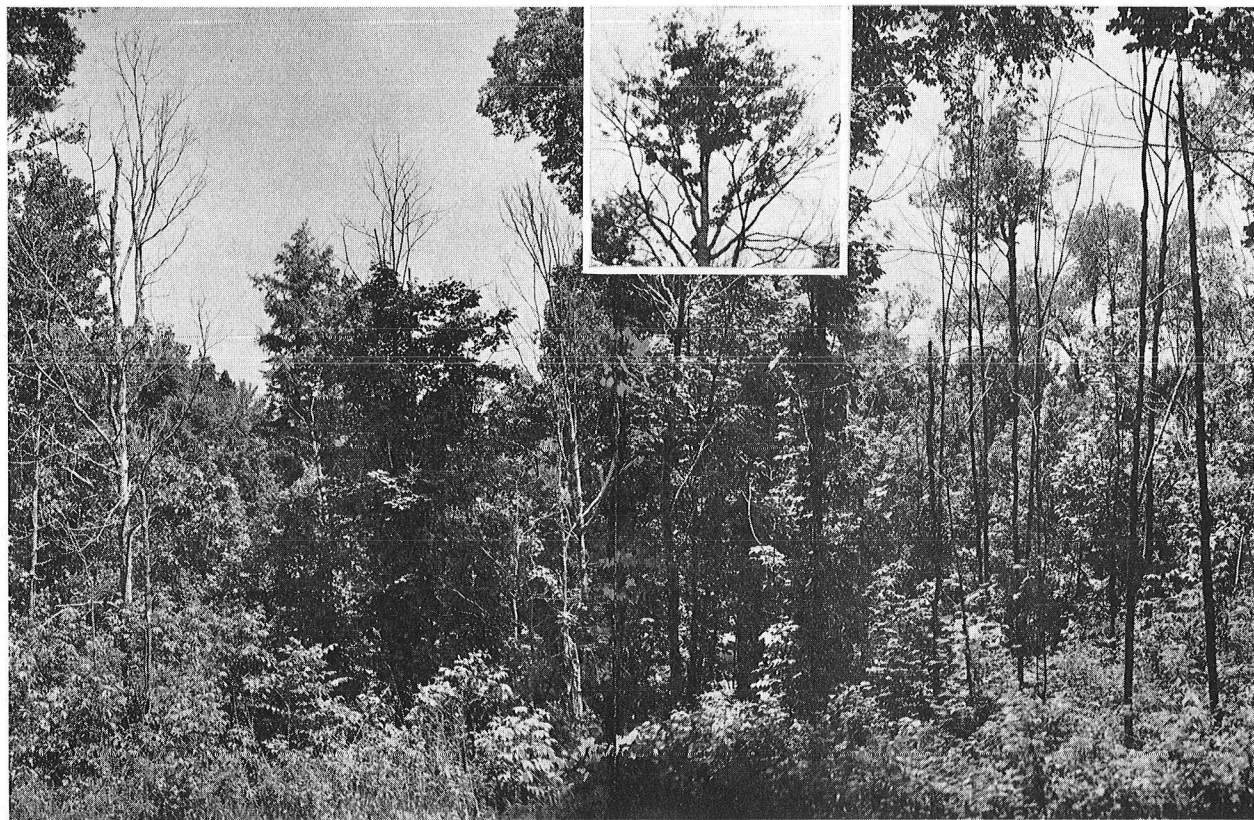
traced over a period of 3 years. On affected trees, additional tissue below initial dead terminal twigs rarely died except on some severely affected branches. A sharp line of demarcation usually occurred between living and dead tissues. In many instances, a narrow band of dark-green discolored sapwood developed at this junction. Occasionally, when the latent buds at the node below a dead terminal failed to develop epicormic sprouts, the branch died back to the next node or to a point where live leaf or sprout tissue had developed. Many saplings had living foliage only on bole sprouts. On badly af-



Part III, Fig. 3. Terminal dieback symptom on a twig collected in September, 1959. The 2-year-old terminal (A) had died by the spring of 1957. The epicormic sprout tissue (B) initiated growth the spring of 1957 from a latent bud on the now 6-year-old basal portion of the twig.



Part III, Fig. 4. Blighted tree with "tufted" appearance due to the abundant epicormic sprout foliage produced from latent buds at nodes.



Part III, Fig. 5. Blighted stand with symptoms of maple blight, including branch dieback; abundant tufted foliage on epicormic sprouts; dead saplings in the exposed understory along with a lush ingrowth of raspberries, nettles, grasses, and broad-leaved weeds.

fected trees, bole sprouts occasionally wilted and died suddenly in midsummer or late summer and remained attached to the tree for some time.

Within Stands

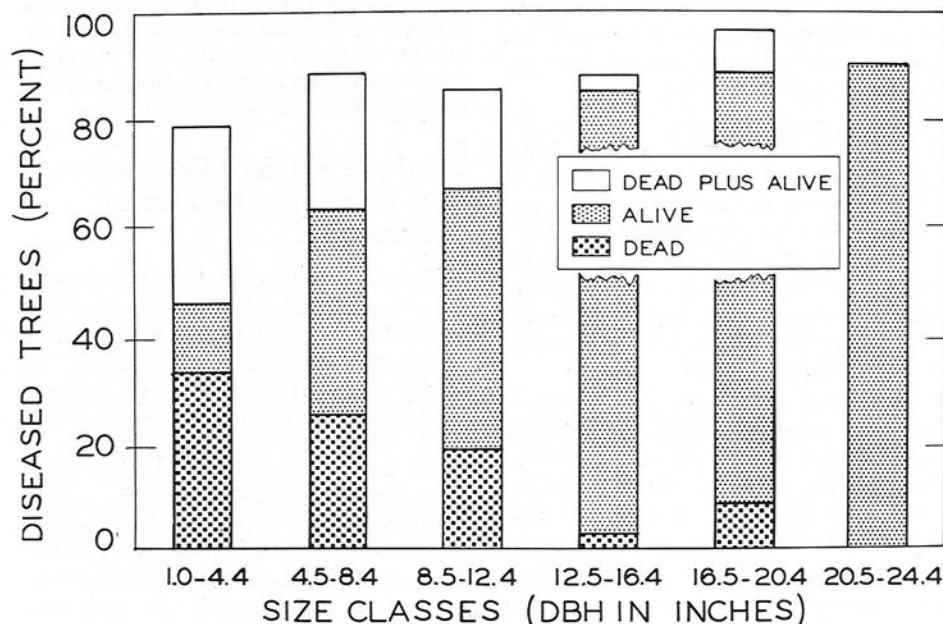
Measurements of stand conditions were taken each year in permanent study plots. Disease development was slight in 1958 compared with the apparently severe disease development of 1956 and 1957. Thus, in these plots during 1958, no trees died, and there was an overall increase of only 4% in the number of diseased trees. In 1959 and 1960, mortality of some of the most severely diseased trees occurred. Generally, however, the still-living, diseased trees tended to improve in appearance with the dropping off of dead twigs and branches or a masking of dead tissue by new sprout foliage. Thus, little additional foliage symptom development occurred after 1958 although tree mortality continued.

More seedlings and saplings died than larger trees, although a higher percentage of the large, living trees was dis-

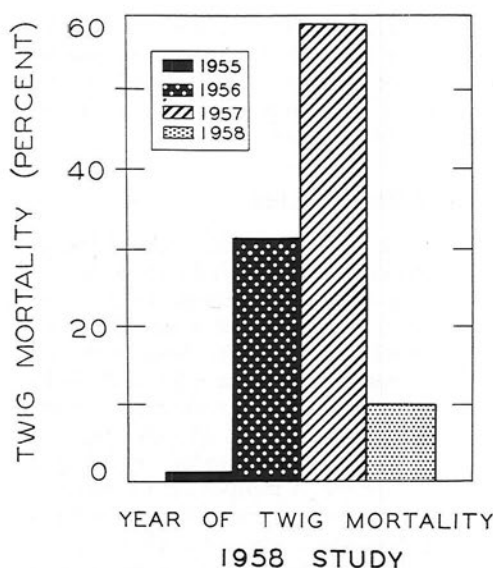
eased (Fig. 6). On a per stem basis, however, the effect of the disease was greatest upon the smaller trees because of the relatively high proportion of stems in the lower dbh classes.

In Different Areas

The presence of dead terminal twigs in the crown of blighted trees was a common symptom of maple blight. The abrupt transition between the dead and apparently healthy living tissue permitted a determination of the year that death of the terminals had occurred by comparing the number of growth rings of the dead end with those of the adjacent living portion. A comparison of different lots of 50 twigs each, collected in 1958 from 4 major blight areas (Fig. 1) indicated that disease development was most severe in 1956 and 1957 (Fig. 7), and that the severity in any one year varied in different locations (Fig. 8). Thus, the percentages of twig mortality in 1956 were highest in the most easterly area (Patten Lake Area) and decreased with increasing distance to the west. In 1957,



Part III, Fig. 6. Disease incidence in different size classes. Data were taken August, 1958, on 848 trees located in 6 study plots.



Part III, Fig. 7. Twig mortality in different years determined by growth-ring counts of 200 diseased twigs collected from 4 locations in 1958.

the highest twig mortality occurred in the most westerly location (Volkler's Spur Area) and decreased with distance to the east. Twig mortality in 1958 was greatest approximately midway between the eastern and western locations, and decreased in either direction.

The 4 severely diseased areas of the above study were sampled more intensively to determine the relationship of disease severity to stand composition and density. The average percentage of crown involvement at the time of sampling increased with a decrease in the relative density, dominance and frequency of sugar maple in the stands prior to the occurrence of maple blight (Fig. 9).

The effects of the disease upon the 4 stands were determined (Fig. 10). Maple blight caused reductions of 25-66% in the numbers of sugar maple trees per acre; and of 18-60% in the basal area of sugar maple per acre.

Although the effects of maple blight were primarily upon sugar maple, other species were affected indirectly. For example, deterioration of the residual yel-

low birch resulted from opening the stand by blight and salvage cutting. In 1961, three years after maple blight appeared, dieback of the birch was severe in some areas. In addition, opening of the stands encouraged establishment of more intolerant species, particularly American elm.

Results of Isolations and Inoculations

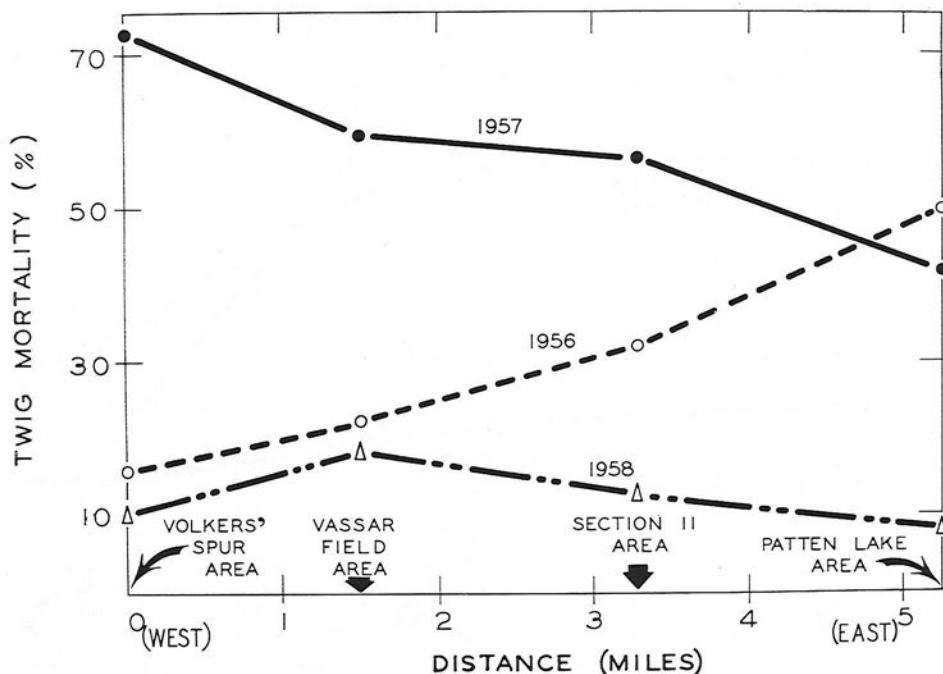
Many different fungi and bacteria were isolated from various tissues of the diseased trees, although none of them exclusively from one particular tissue.

Representative isolates, which included such genera as *Fusicoccum*, *Phoma*, *Dothiorella*, and *Phomopsis*, inoculated into healthy maple saplings produced none of the symptoms of maple blight. Discoloration of the outer sapwood commonly developed immediately above and below the wounds whether inoculated or not.

No evidence for the presence of viruses in blighted trees was obtained by the common transmission procedures. None of the virus indicator host plants or inoculated maple seedlings developed symptoms. Different plant parasitic nematodes were found in the root zones of maples with and without disease symptoms (Riffle, 1962 and 1963).

Results of Artificial Defoliations—Host Responses the Year of Treatment

The fact that maple blight developed only in previously defoliated stands suggested that insect defoliation might have contributed to disease development. To clarify this possible relationship, different groups of 3-20 saplings each were defoliated completely at 1-week intervals in 1958, and at 2-week intervals in 1959. Biweekly examinations of each sapling defoliated in 1958 gave only a general picture of host responses. In 1959, different groups of 3 saplings each were defoliated at 3-4 day intervals. At each date, records of host responses were taken for each of the saplings defoliated previously.



Part III, Fig. 8. The percentages of 50 twigs which died in each of 4 areas in 1956, 1957, and 1958. The areas are plotted according to the distance separating them along an east-west transect.

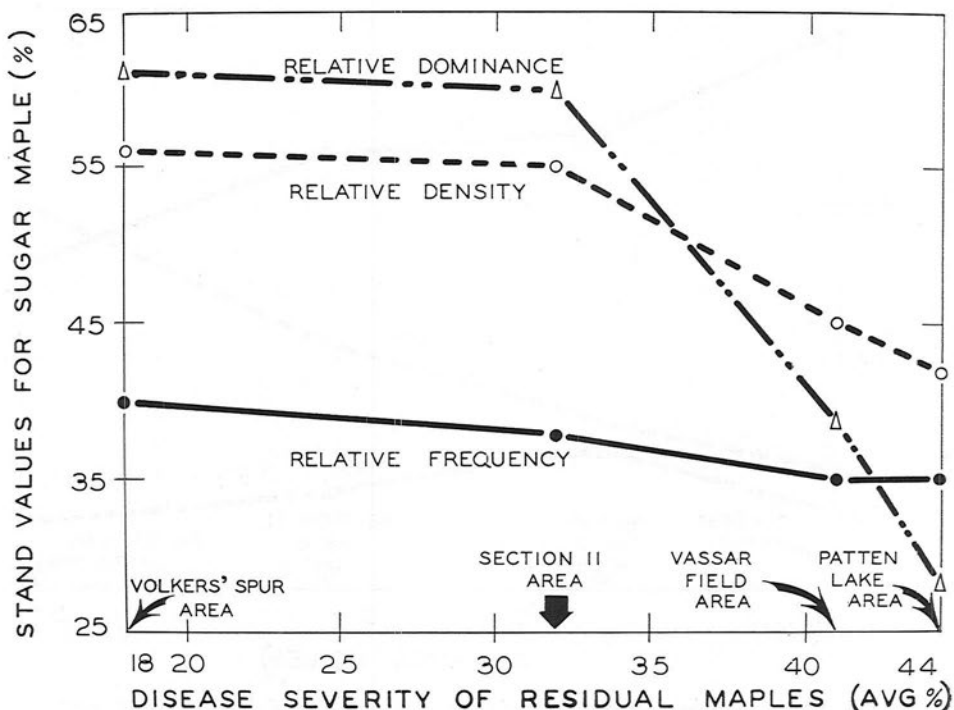
Marked responses to defoliation occurred the year of treatment. Petiole abscission began approximately 6-10 days following removal of the leaf blades, and continued for 9-12 days. Usually before abscission was completed, a few terminal buds began to swell and to elongate. Bud-break and leaf expansion followed. Thus leaf expansion started about 21-24 days after defoliation. Sometimes petiole abscission, bud elongation, and leaf expansion occurred simultaneously on different parts of the same sapling.

The first terminal buds to initiate growth were on upper crown branches. As the season progressed, buds on mid-crown and finally on lower crown branches responded. Lateral buds rarely responded. A full complement of new leaves was never produced (Figs. 11, 12). The number of buds which responded and therefore the number of leaves produced were less following each successive defoliation (Fig. 12). The trees which were

defoliated completely a second time 9 weeks after their first defoliation, re-foliated again only slightly. The few leaves produced were small and chlorotic and developed from terminal buds that had not responded following the first defoliation. Buds on saplings in the open responded to a greater degree than did those on saplings in the shade (Fig. 12).

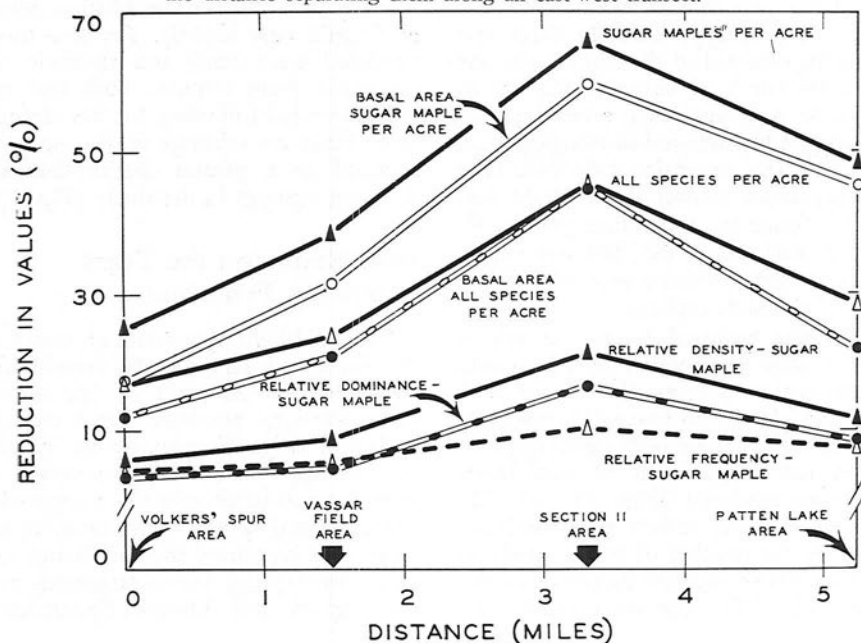
Host Responses the Years Following Treatment

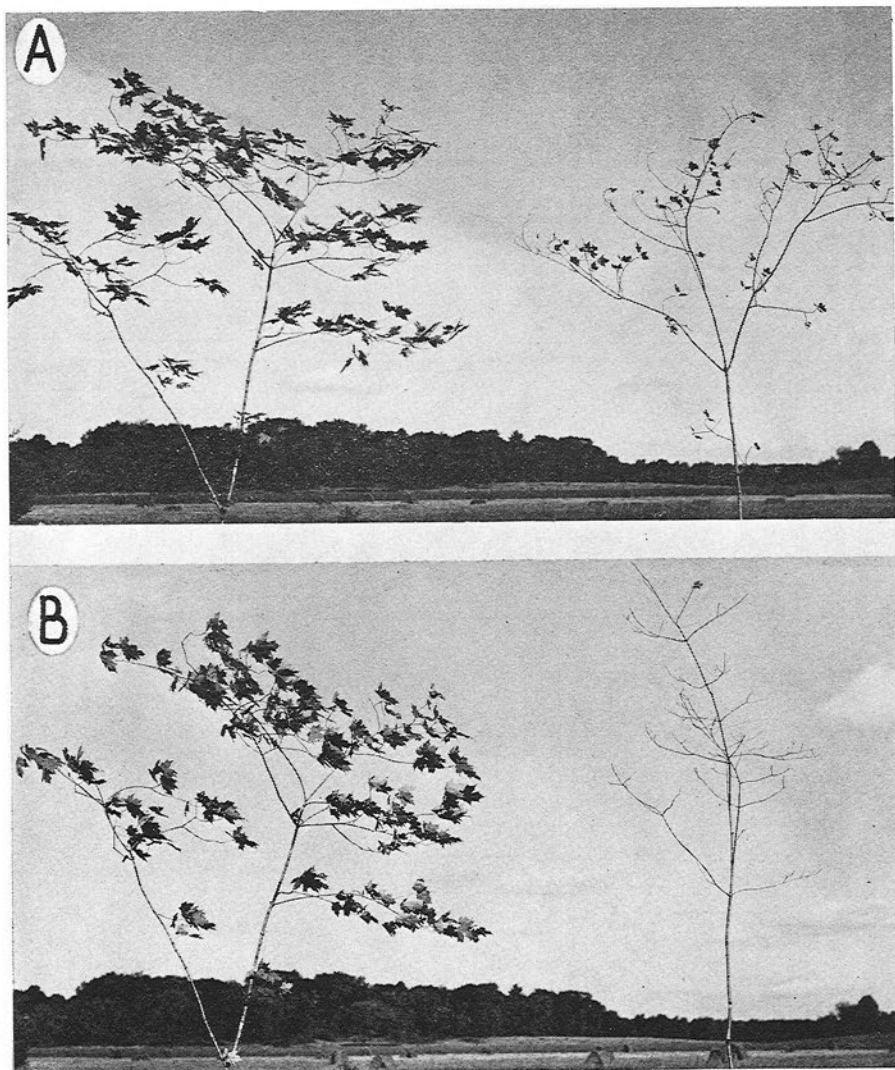
Typical blight symptoms appeared on the defoliated saplings the season after treatment. At the start of the season, many saplings possessed dead terminal buds and twigs, particularly on branches of the upper crown. Latent buds on branches and boles gave rise to epicormic sprouts. Basal sprouts were common, and sometimes supported the sole living foliage of the sapling. Leaves frequently were small, sparse, and chlorotic. Sprout leaves



Above: Part III, Fig. 9. Stand values for sugar maple prior to maple blight related to disease severity of the trees remaining in 4 maple blight areas after salvage cuts. Disease severity was expressed as the average percentages to which the trees were affected.

Below: Part III, Fig. 10. The effects of maple blight expressed as a reduction in stand values for sugar maple and for all species. The 4 areas studied are plotted according to the distance separating them along an east-west transect.





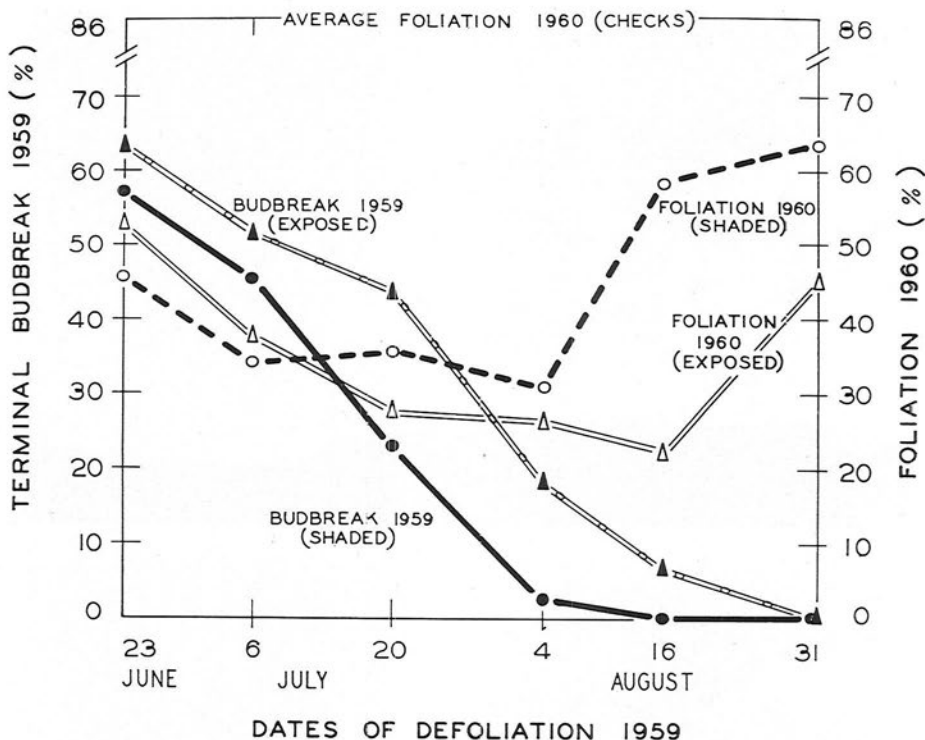
Part III, Fig. 11. Refoliation of understory saplings defoliated on June 23, 1959, (A) and on July 20, 1959, (B). Saplings on left are nondefoliated controls. Pictures were taken on September 24, 1959.

often wilted and died as the season progressed. In some cases, death of the entire sapling occurred. Most of the saplings twice defoliated in 1958 were dead in 1959. Those still alive had only a few living bole or basal sprouts.

Symptom appearance was associated closely with the place of defoliation on the tree. Thus, dead terminal bud-groups and small, sparse, chlorotic leaves were

produced only on the previously defoliated members of paired branches. No effects appeared on the undefoliated check branches.

Bud mortality varied with date of defoliation in the previous year. Terminal bud-group mortality increased with date of defoliation from June through early August, after which it decreased (Figs. 13, 14). Thus, a "critical" period oc-



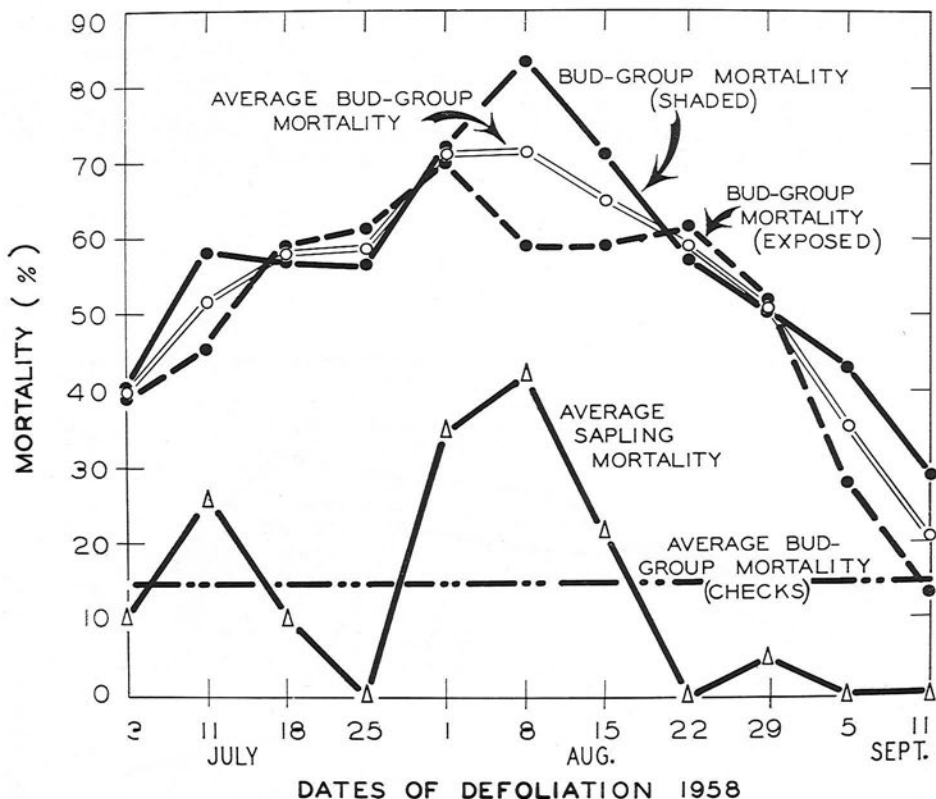
Part III, Fig. 12. Terminal budbreak (1959), and foliation (1960) following manual defoliation of sugar maple saplings at different dates in 1959. Comparisons of budbreak (measured Sept. 25, 1959) and foliation (measured June 23, 1960) were made among different groups of 20 trees each growing either in opened (exposed) or in dense stands (shaded).

curred for defoliation of sugar maple from mid-July to early mid-August. The highest bud mortality occurred on those saplings in the open in 1959 (Fig. 14), and in the understory in 1958 (Fig. 13).

Early fall frosts in September of 1958 injured newly refoliated tissues of saplings in the open but not of saplings in the understory. In 1959, temperatures were recorded in the defoliation plots. From September 11-18, air temperatures of 32°F. or below occurred on 5 days, for 40 hours, with a minimum temperature of 24°F in the open defoliation plot compared to 1 day, for 6 hours, with a minimum of 32°F in the understory defoliation plot.

Tree Mortality

Death of saplings was greatest in those defoliation series with the highest bud mortality (Fig. 13). Several anomalies in the curve, however, reflecting results of defoliations on July 11, 18, 25, and August 22, and the vigorous appearance of the still-living saplings of several different series suggested that causes other than defoliation alone might be responsible for sapling death. Plotting all trees and stumps in defoliation plots revealed that the dead defoliated saplings were associated with nearby stumps, and previously dead trees and saplings. Thus, the defoliated saplings which had died by 1959 were closer (within 8 feet) to the



Part III, Fig. 13. Terminal bud-group mortality and sapling mortality of different 10-tree groups of maple saplings manually defoliated once in 1958. Bud-group mortality was compared on saplings in opened stands (exposed) and in dense stands (shaded). Readings were taken July 30, 1959.

nearest previously dead sapling, tree, or stump than were living defoliated saplings (12 feet away). As a result pockets of dead trees formed around stumps or previously dead trees. This pattern of dead trees continued in 1960 and 1961 (Fig. 15), and suggested that root rot fungi, with root systems of dead trees or stumps for a food base, were possibly responsible for additional tree death.

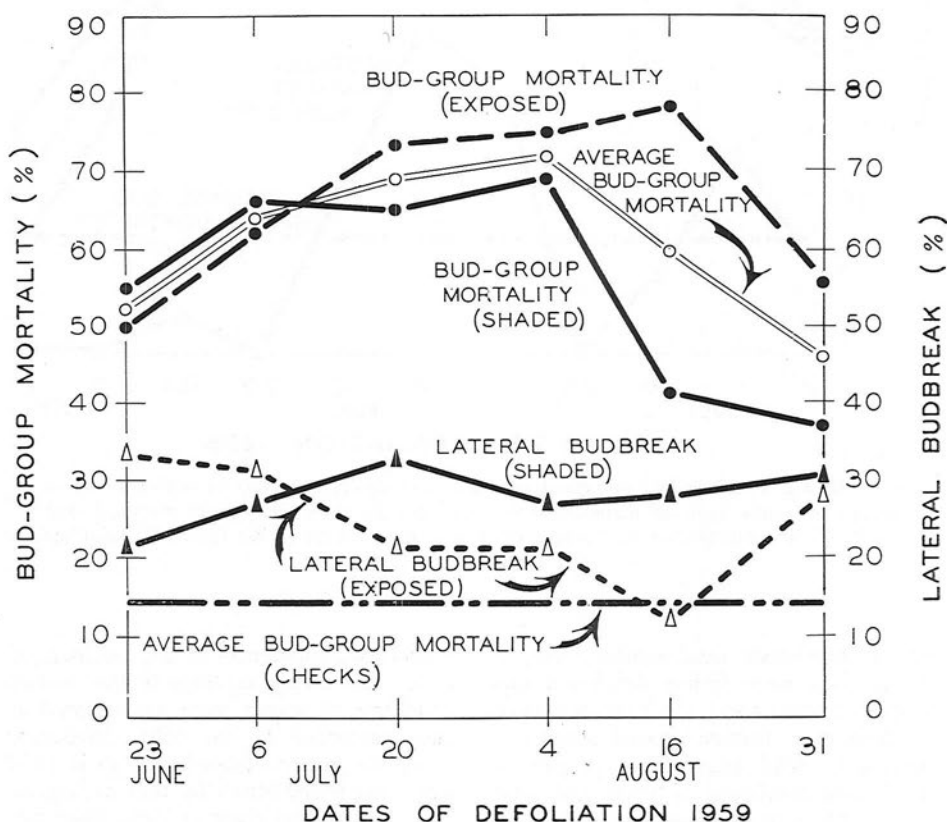
To clarify the possible relationship of root rots and defoliation, the trees and saplings in 2 plots encompassing known root rot pockets were numbered and their positions were mapped. All the maple saplings in these plots were defoliated completely in July 1959. Although by

July 1960, differences in the distances of killed and living saplings to the nearest dead tree or stump were not as great as those recorded in the 1958 defoliation plots, the pattern of dead saplings in 1960 again suggested attack by root pathogens. This pattern continued in 1961. Root collars and root systems of previously dead trees and stumps as well as of the several dead, defoliated saplings examined invariably supported fans and rhizomorphs of *A. mellea*.

Additional evidence to support the possibility that defoliated trees were more susceptible to root rot fungi was obtained upon examination of stumps of blighted and nonblighted trees in several areas. More (70%) stumps of blighted

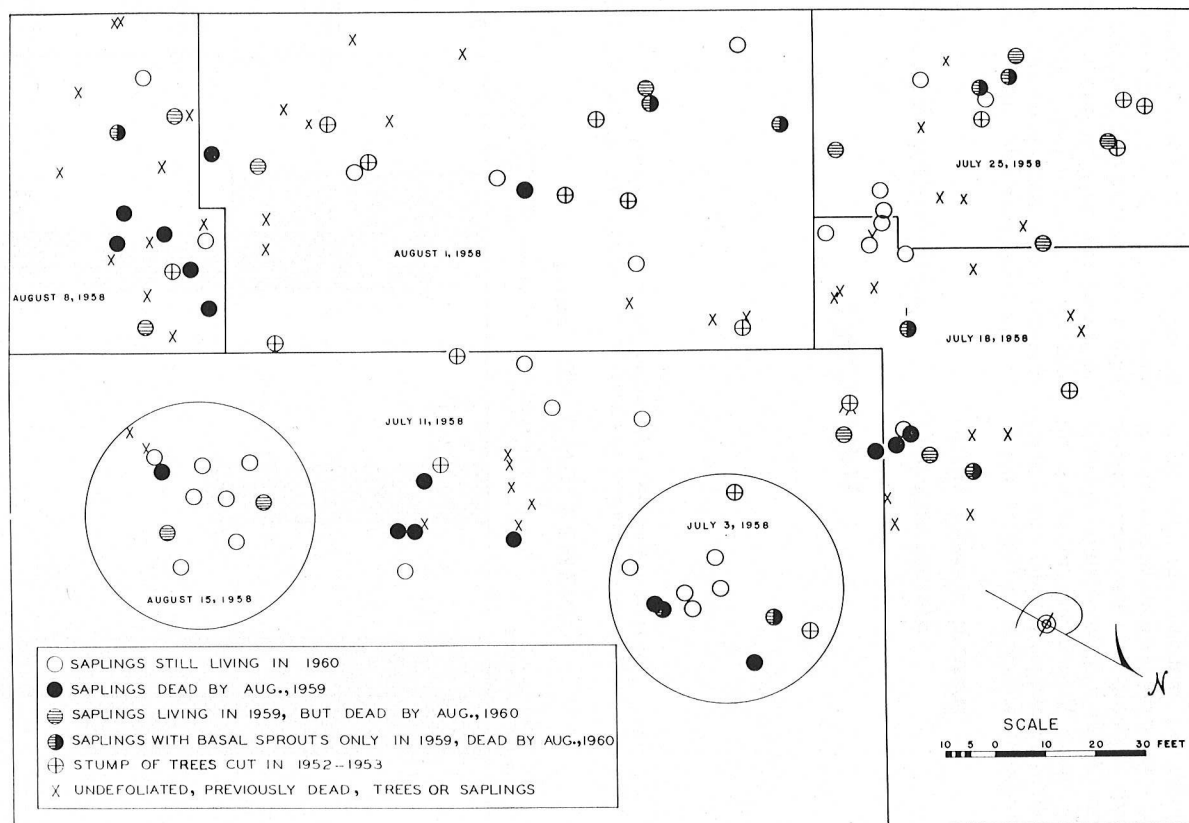
trees were attacked by *A. mellea* than were stumps of nonblighted trees (32%). Likewise, the stumps of blighted trees were more severely invaded by this fungus than were those of nonblighted trees (Fig. 16). In contrast, fewer

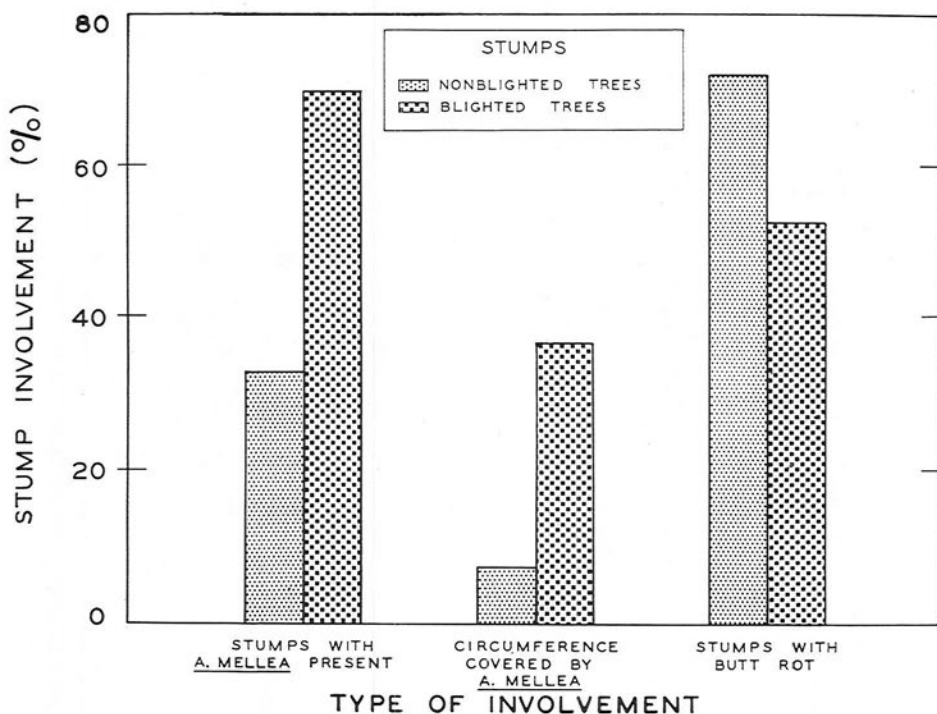
stumps of blighted trees (62%) were attacked by other butt rots than were stumps of nonblighted trees (72%). This latter situation reflected the enforced salvage cutting of smaller and younger trees than would be cut normally.



Part III, Fig. 14. Terminal bud-group mortality and lateral budbreak following manual defoliation of sugar maple saplings at different dates in 1959. Comparisons of bud-group mortality and budbreak (measured June 23, 1960) were made among different groups of 20 saplings each growing either in opened (exposed) or dense (shaded) stands.

Part III, Fig. 15. Pattern of sapling mortality in years subsequent to manual defoliation in 1958.





Part III, Fig. 16. The involvement of stumps of blighted and nonblighted trees with *Armillaria mellea* and with other miscellaneous butt rots.

Discussion

Nature of the Maple Blight Disease

Maple blight appeared suddenly in northern hardwood forests of northeastern Wisconsin and then subsided as abruptly as it had appeared. This was shown by several results: (1) The greatest terminal dieback occurred in 1956 and 1957 with little damage before or since. (2) During the 3-year study period individual branches showed little subsequent tissue death; a continual recovery from symptoms occurred in all of the study plots; and boundaries of diseased areas did not enlarge in the stands mapped in 1958.

Probable Nature of the Disease Incitant

The pattern of widespread disease incidence and rapid development suggested the nature of the inciting agent. Thus, possible primary incitants might include abiotic causes such as drought, changes in water table, or toxic gases; or a biotic agent with the potential for rapid increases and decreases in population over wide areas. The causal agent affected and incited symptoms in sugar maple only, regardless of tree size, vigor, or age; with an immediate host response. The only known disturbance to these stands was

the insect defoliation which occurred in 1955, 1956, and 1957. Thus, it became a matter of determining the effect of defoliation on maple.

Insect Defoliators as Primary Incitants of Maple Blight

Several lines of evidence supported the premise that defoliating insects were the primary inciting agents responsible for maple blight: (1) Maple blight occurred only in areas which had been previously heavily defoliated by the maple webworm, *Tetralopha asperatella*. Maple blight was not attributed to defoliation immediately because no previous record existed to indicate that sugar maple would suffer serious damage as a result of one or two insect defoliations. Nor was the critical timing of such defoliation appreciated. (2) No symptoms of maple blight resulted from inoculations with fungi or bacteria isolated from diseased trees, or from attempts to transmit viruses. (3) Typical maple blight symptoms were produced the year following mechanical defoliations of sugar maple saplings. (4) Symptoms of maple blight exhibited by the defoliated saplings were similar to those which occurred on other tree species following natural and artificial defoliations (Batzer, 1955; Batzer *et al.*, 1954; Rose, 1958; Wallace, 1945) and/or frost damage (Rose, 1958; Spaulding, 1946).

A "critical" period of several weeks in length occurred for response to the defoliation of sugar maple in Florence County. Thus, bud mortality increased with the date of defoliation the previous year through early August, after which it decreased. It is of significance that this period coincided with the peak of the activity period of *T. asperatella* in the maple blight areas (Giese, 1960).

Death of certain saplings occurred after one complete defoliation. The spatial distribution of the killed saplings indicated that factors other than defoliation alone contributed to mortality.

Contributing Factors

The aggregation of dead saplings in several defoliation plots suggested that

root rots were involved in the death of some saplings following defoliation. Several studies implicated *A. mellea* as a contributing factor: (1) Stumps of blighted trees, which had been defoliated naturally prior to cutting, were attacked more frequently and more severely by *A. mellea* than were stumps of nondefoliated trees. (2) The root collar regions of stumps and of previously dead trees and saplings in the defoliation plots usually were attacked by *A. mellea*. (3) The root systems of the dead, defoliated saplings that were examined frequently revealed the presence of rhizomorphs or mycelial fans of *A. mellea*. (4) The continual death of saplings in "pockets" for at least 3 years after defoliation suggested a progressive attack of the defoliated saplings by root rots. These observations suggested that the root collar tissues of defoliated trees were more suitable to attack by *A. mellea* than were those of nondefoliated trees. Defoliation and the subsequent refoliation may have altered the carbohydrate content of the root collar tissues. Bliss (1941) and Leach (1937) have shown that rhizomorphs of *A. mellea* are its principal means of infection and that they develop at a critical substrate C/N ratio (Garrett, 1951). The possibility exists that susceptibility also varies with a critical C/N ratio.

Environment also appeared important in the disease complex. Frequent and severe early fall frosts occurred in Florence County. In 1958, when few early fall frosts occurred, mortality of buds and twigs was about the same for saplings defoliated in the open and in the closed stand. Exceptions were the defoliation of August 8 and August 15, when bud mortality was greatest on the understory saplings. These particular groups of saplings, however, were located in an opening created by the removal of two large trees in 1952. More frequent and severe frost would occur in such an opening than under the adjacent canopy, or in the open (Geiger, 1950). In 1959, earlier, more frequent, longer, and more intense frosts were recorded in the open plots than in the understory plots. Correspondingly, bud mortality was highest in 1959 in the

open plots. The occurrence and severity of fall frosts, and the severity of bud and twig dieback symptoms thus appeared to be related partially to the nature of the overstory. The severity and frequency of fall frosts and perhaps of winter cold in northerly Florence County might help to explain why only limited damage to buds and twigs followed insect defoliation in more southerly areas of Wisconsin.

Relationships of Stand Factors to the Development of Maple Blight

In 1958, the stands with the most severely diseased residual trees were those stands which had had the lowest relative

densities, dominances, and frequencies of sugar maple trees prior to maple blight. The low-density stands were probably most suitable for the build-up of webworms due to the more favorable temperature and light conditions in the understory (Giese, 1960). Even in stands of low density, sugar maple was present in high numbers, as was shown by the very slight reductions in relative frequencies of maple following maple blight. Stands opened by heavy cutting generally had high populations of vigorously growing seedlings and saplings of maple—the preferred host of the webworm. The understories of such stands would also be more exposed to early fall frosts.

Summary

Maple blight, first reported in 1957 in northeastern Wisconsin, caused deterioration and mortality of sugar maples growing in managed stands of mixed northern hardwood forests. Variable insect defoliation of maples had occurred for one to several years prior to the appearance of the disease. The disease was severe in 1956 and 1957. Generally, affected trees have shown continuing recovery since 1958. Symptoms included dead terminal buds and twigs; small, sparse, chlorotic foliage; formation of branch and bole sprouts; and sometimes death. Inoculations with representative fungi and bacteria isolated from diseased trees, and transmission tests for viruses failed to produce maple blight symptoms. Typical symptoms developed the year following

mechanical defoliation of maple saplings; were restricted to those branches that were defoliated; and were especially severe on saplings defoliated from mid-July to mid-August. Tissues which refoliated the year of defoliation were susceptible to damage by local fall frosts. Thus, saplings defoliated in exposed areas suffered more damage than did saplings protected by dense overstories. Defoliated saplings which died appeared associated with adjacent stumps or previously dead trees and saplings and were attacked by root-rot fungi, especially *Armillaria mellea* (Vahl.) Quel. Stumps of blighted trees were attacked more frequently and to a greater extent by *A. mellea* than were stumps of nonblighted trees.

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PART IV.

Defoliation and the Genesis of Maple Blight¹

Ronald L. Giese², Joseph E. Kapler³ and Daniel M. Benjamin⁴

Introduction

EPIPHYTOTIC POPULATIONS of the leaf rollers, *Sparganothus acerivorana* MacKay and *Acleris chalybeana* (Fern.), and the webworm, *Tetralopha asperatella* (Clem.), resulted in partial to complete defoliation of sugar maples in northern hardwood forests of Florence County, Wisconsin in 1955, 1956 and 1957. Maple blight appeared on about 10,000 acres there in 1957 and 1958 (Fig. 1). This was not a local phenomenon, as the same complex of defoliating insects was present in Iron County in outbreak in 1957, 1958 and possibly prior to those years (Fig. 2). The area of trees

stripped by insects in Iron County was about 2 acres and the sapling and tree mortality was nearly complete. The impact on sugar maple following insect activity appeared similar to that of the Florence County blight area.

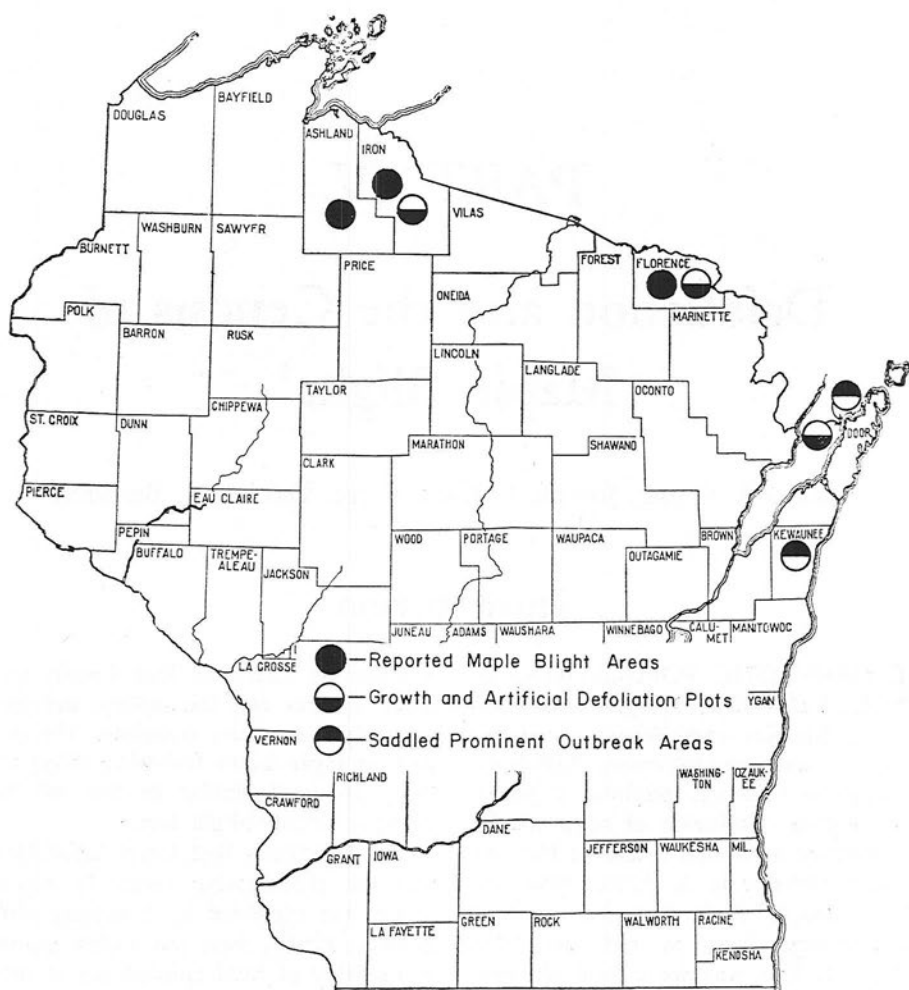
The hypothesis that insect defoliation was the predisposing factor to maple blight was suggested by 2 striking phenomena. Firstly, there was a close spatial relationship of local epiphytotics to subsequent maple blight areas. Secondly, a cessation in the development of maple blight came with the collapse of outbreaks of defoliating insects.

¹ This project was supported in part by the Northern Hardwood and Pine Manufacturers Association, the Wisconsin Conservation Department and the U.S. Forest Service, Lake States Forest Experiment Station; to these agencies, the authors wish to express their appreciation.
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Part IV, Fig. 1. Distribution of maple blight and defoliation study areas.



Part IV, Fig. 2. Maple blight in a second growth stand of sugar maple in Iron County, Wisconsin.

Review of Literature

The growth impact caused by defoliation has been investigated intensively for several coniferous and hardwood hosts. Usually, studies were directed primarily toward an evaluation of reduction in radial increment and particularly to the coniferous trees (Mott, Nairn and Cook, 1957). Mechanical defoliation of a deciduous conifer, tamarack, *Larix laricina* (DuRoi) K. Koch, caused mortality and growth loss (Graham, 1931). The effect of defoliation on growth of longleaf pine seedlings was studied by Bruce (1956) with the use of an artificial defoliation technique. Artificial defoliation of jack pine had pronounced effects in a Quebec study (O'Neil, 1962); "Current foliage was found essential for the maintenance of normal height, diameter, and shoot growth..." Complete defoliation caused tree mortality; partial defoliation elicited

extra adventitious growth and increment reductions.

Most research on defoliation effects on hardwoods has been limited to the pioneer species. For example, the effects of forest tent caterpillar, *Malacosoma disstria* Hbn., defoliation on aspen, *Populus tremuloides* Michx.; have been studied in detail. Increased frequency of defoliation by the tent caterpillar caused an increase in crown dieback, but did not result in mortality (Batzer *et al.*, 1954 and Batzer, 1955). A general decline in tree vigor accompanied the dieback and 90% of the normal growth was lost during the third year of complete defoliation (Batzer and Waters, 1956). Hodson (1941) reported 20 to 80% tree mortality, with amount of damage being influenced by site and age and the number of complete defoliations. Within areas of Saskatchewan

forest tent caterpillar outbreaks greater mortality of trembling aspen was incurred by suppressed trees in the lowest size class (1-4 inches dbh) than by individuals with diameters of 5 inches (bh) or larger (Hildahl and Recks, 1960). Rose (1958) studied defoliation effects on foliage production and radial growth and reported refoliation occurred in stands where trees had been completely defoliated. The refoliated leaves were about normal in size, but were limited to the periphery of the crown. Radial growth of aspen ceased after defoliation, but resumed when refoliation occurred (Dils and Day, 1950; Barter and Cameron, 1955).

Minott and Guild (1925) examined the effects of defoliation by the gypsy moth, *Porthetria dispar* (L.), and found 4 species of *Quercus* lost an average of 36.5% of the foliage (ranging from 0 to 100%) per year for a 10-year period. By the end of this period, 47% of the trees were dead and a 38% loss of growth was evident. Collins (1961) studying the effects of the same insect, observed refoliation in oak species. Varley and Gradwell (1962) reported that *Quercus robur* L. in England is commonly defoliated by *Operophtera brumata* L. and *Tortrix viridana* L. Even though the trees refoliated, summer increment reduction was highly correlated with caterpillar density.

Caroselli (1957) investigated the effect of artificial defoliation on 15 sugar maple saplings to determine the effect on inci-

dence and development of *Verticillium* spp. After 60 days, the defoliated trees had produced a new flush of leaves. Neither defoliated inoculated nor defoliated non-inoculated trees had wilt or dieback symptoms. The non-defoliated inoculated trees had a mean wilt condition of 42%. One year later, tissue samples of defoliated trees yielded the fungus in 80% of the trees, but isolations were possible only from the source point of inoculation. Caroselli concluded that defoliation suppressed the incidence of *Verticillium* wilt, and inhibited its spatial development.

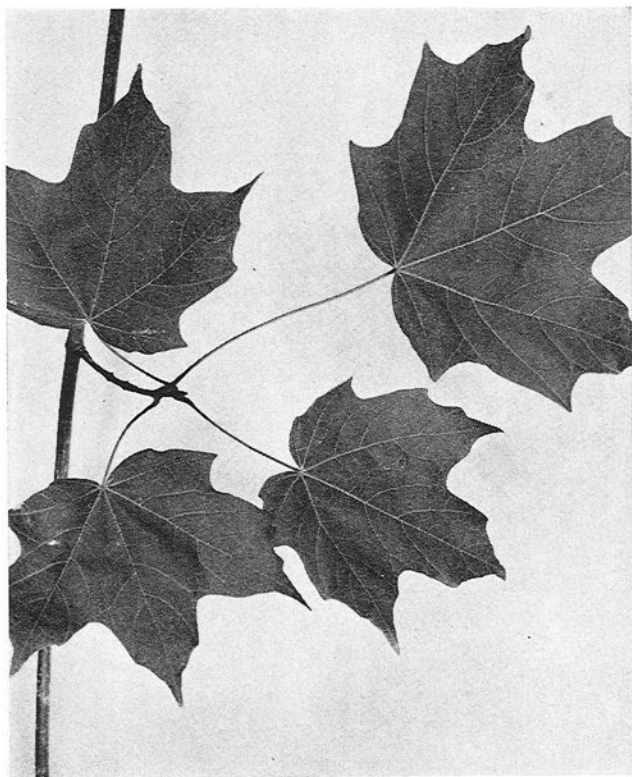
Defoliation of conifers and pioneer deciduous trees may be reflected by dieback, reduction in increment and by death. It had been thought by many forest scientists that partial and complete defoliation in the climax hardwoods could be tolerated for several successive seasons with little if any deleterious effects. Consequently, since the area afflicted with maple blight had a history of previous defoliation, and this defoliation immediately preceded the occurrence of the disease, it was postulated that insect defoliation predisposed the trees to blight.

Within the areas stricken with maple blight, the insect populations had declined to or below the general equilibrium position precluding the evaluation of progressive natural defoliation of sugar maple. Therefore, mechanical stripping of saplings was utilized to simulate insect attack and to determine the effects of defoliation on growth.

Material and Methods

Sugar maples were artificially defoliated to varying degrees by removing the leaf blades from the petioles of naturally occurring groups of 2 to 4 leaves (Fig. 3). The petioles were left intact and no damage resulted to the dormant buds. Trees of all crown classes were included in the study. In a closed stand area (T39N R17E S20, 21), understory saplings averaging 10 feet in height were utilized. In 1958, treatments were established on a weekly schedule beginning on July 7 and

continued until August 26. Each defoliation plot was comprised of 5 treatment levels and a control. Trees in different 5-tree groups were bent over and defoliated sectionally as follows: completely, upper two-thirds, lower two-thirds, and upper one-third, and lower one-third of the crown. Five non-defoliated trees were bent over to serve as controls (Fig. 4). No trees were defoliated more than once per season. Three-fifths of the 1958 treated trees were defoliated on the same



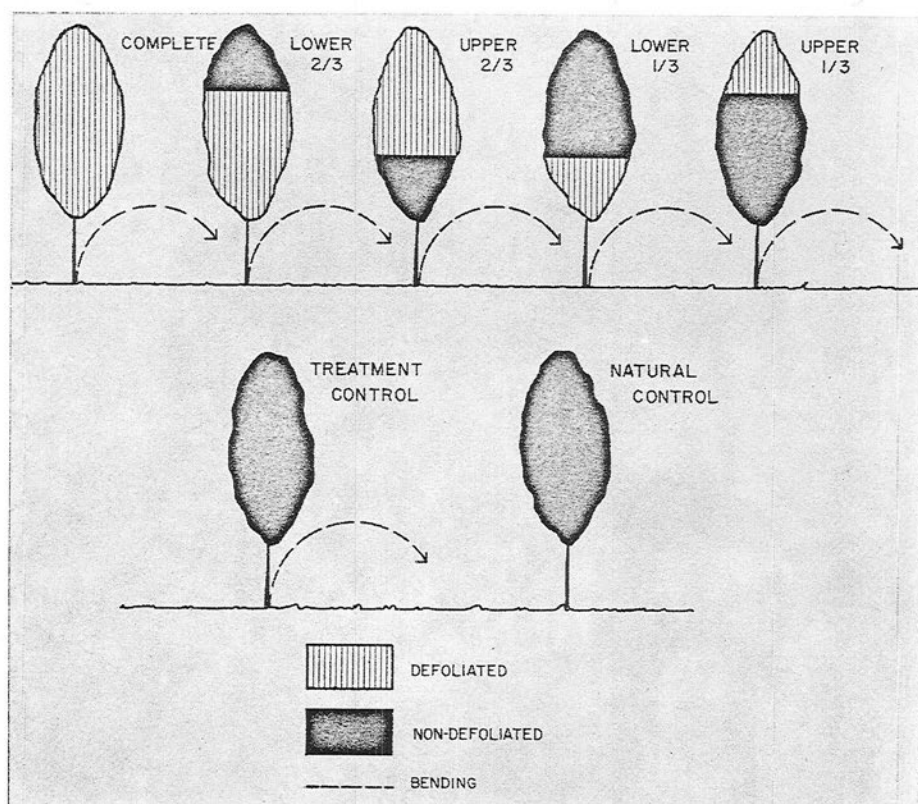
Part IV, Fig. 3. Growth pattern of a sugar maple foliar unit consisting of naturally occurring 4 leaf groups.

date 1 year later to simulate an insect outbreak a second year. In 1959, defoliation began on June 7 and continued until September 15. Also, one each of the type of defoliation plots described above was established in Door and Iron Counties, Wisconsin on July 28 and 29, 1959 (Fig. 1). During this treatment year, a series of non-bent, non-defoliated trees was added as untreated checks.

The second stand type defoliated was an open, second growth area (T40N R16E S9) dominated by sugar maple saplings. The upper limit of the canopy seldom reached more than 40 feet in height. Four 1/40-acre plots were established. Once each week in August 1958 all saplings on each plot were completely defoliated. Saplings ranged from 5 to 38 feet in height; dominant, suppressed and intermediate trees were treated. Concur-

rently, in this area, qualitative studies were initiated to detect the response to defoliation of hardwoods other than sugar maple under the open stand condition. In 1959, this study was expanded to include the complete defoliation of basswood, *Tilia americana* L., yellow birch, *Betula alleghaniensis* Britton, and ironwood, *Ostrya virginiana* (Mill.) K. Koch.

Three types of evaluation were employed in the sugar maple study. The most reliable method was the actual (numerical) determination of living and dead buds. In northern Wisconsin, sugar maple normally produces leaves in units of 4, comprised of 2 groups of opposite leaves (Fig. 3). This *normal terminal foliar unit* includes 4 leaves, a terminal bud and 4 axillary buds. Epicormic sprouts also were recorded in this numerical evaluation. An *epicormic foliar unit*



Part IV, Fig. 4. Treatment regimes used in artificial defoliation investigations on sugar maple.

is defined as a group of leaves that arose from other than terminal or axillary bud origin and is 5 years or less in age. Units that originated as epicormic sprouts, but have persisted more than 5 years, were considered as normal terminal units. Time of epicormic foliar unit production was recorded, based upon a 2-group delimitation in which the epicormic unit arose "prior to" or "following" treatment. The epicormic foliar unit ratio (E) was then calculated from the formula:

$$E = \frac{\text{new (post-treatment) epicormic foliar units.}}{\text{old (pre-treatment) epicormic foliar units.}}$$

When the epicormic foliar unit ratio was greater than one, more epicormic foliage was produced in the current year than in

the previous 4 years. Conversely, when the ratio was less than one, less epicormic foliage was produced in the same time.

Refoliation evaluation followed a numerical technique similar to the above. Leaf dimensions were determined from linear measurement along the main longitudinal vein from the leaf apex to the base of the leaf blade. Unless otherwise noted, all data presented were evaluated on the basis of actual numbers present at the completion of growth in a given season.

In 1960, an 8-level defoliation treatment was initiated on June 9 and continued through September 7; the first 5 levels correspond to those of the 1958 and 1959 experiments. In addition, 1 of 4, 2 of 4 and 3 of 4 leaves of the 4-leaf unit were removed from over the entire crown. This approximated an uni-

form crown defoliation at various degrees and simulated removal of chlorophyll-bearing tissue by solitary insects such as leaf rollers. It contrasts with the sectional crown defoliation that is best compared to leaf loss caused by a colonial insect such as the webworm.

At the end of the 1960 growing season, an evaluation of impact was conducted for trees defoliated earlier in the season. Trees that produced the greatest amount of refoliated growth were given a rating of 5, while those trees with no refoilation were rated 0. Trees with intermediate refoilation were ranked between these 2 numbers.

A rating system was again used in 1961 to evaluate 1960 defoliation. As most of the treated trees were defoliated in estimated multiples of $1/3$ -crown, an estimation of live crown by $1/6$ -crown classes was conducted. This technique can only indicate broad trends, since it masks the effect of adventitious growth.

A complete sample of tree species was evaluated on a 6/10 acre in Door County in the southwest quarter of S23 T31N R27E. All saplings over 1 inch in diameter were tallied by species, size and vigor. Living trees were classified as "non-affected" or "affected"; the latter classification represented trees manifesting one or more of the maple blight symptoms.

Results and Discussion

The Impact of 1958 Defoliation in Closed Stands

1958 evaluation. Trees stripped early in the 1958 growing season produced a new flush of leaves (refoliation) 30 to 45 days following treatment. These leaves were $1/4$ to $1/3$ the normal size and constituted less than $1/3$ of the normal complement of foliage.

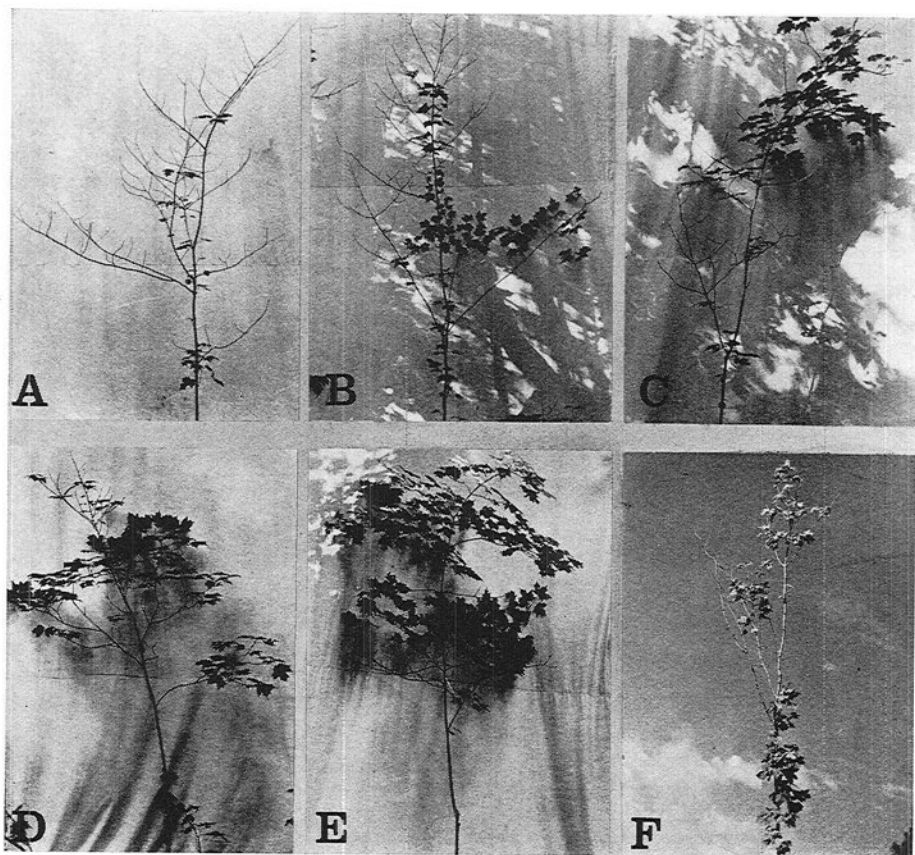
1959 evaluation. One year following defoliation, treated trees differentially exhibited the symptoms of maple blight including 1) *terminal dieback*, 2) *prolific epicormic sprouting*, 3) *wilting* and 4) *occasional mortality*. The impact was approximately in proportion to the intensity of the defoliation the year before, and the site of effect was coincident with the position of the stripped foliage. Complete defoliation caused twig mortality and epicormic growth over the entire crown of the tree (Fig. 5A). Partial defoliation resulted in mortality and adventitious sprouting also, and this was restricted to the treated portions of the crown (Fig. 5B, C, D and E). Open growing, completely defoliated, dominant trees expressed similar symptoms (Fig. 5F).

The impact of defoliation was evaluated quantitatively to obtain more precise

information on the gross influence of time and degree of stripping at varying crown levels throughout the growing season. The foliar unit mortality was nearly proportional to the severity of the treatment (Fig. 6). Completely defoliated trees sustained the greatest twig mortality and the trees on which $1/3$ of the foliage was removed sustained the least twig mortality.

A consideration of the entire crown foliage potential demonstrates inter-relationships between terminal and epicormic foliar units. Grouping of the entire season's data revealed that with an increase in the severity of defoliation, the percentage of foliar unit mortality increased, the percentage of live foliar units decreased and the percentage of new epicormic foliar units increased (Table 1). On the control trees, a mean of 13.1% (ranging from 4 to 20) foliar unit mortality occurred after 1 year.

In most cases, defoliation of the upper crown of suppressed trees resulted in the greatest impact among the partial treatments, but occasionally more twig mortality was caused by lower crown defoliation. Usually, no significant differences could be demonstrated between the foliar unit mortality resulting from the upper and lower crown treatments. The control trees



Part IV, Fig. 5. The impact one year following the mechanical defoliation of sugar maple saplings: (Closed stand defoliation—A, complete; B, upper two-thirds crown; C, lower two-thirds crown; D, upper one-third crown; E, lower one-third crown. Open stand defoliation—F, complete.) (Defoliated July 7, 1958 and photographed August 27, 1959.)

sustained significantly less terminal foliar unit mortality than all treatments. When defoliation took place later in the growing season, the impact diminished to the point where foliar unit mortality for a given treatment was below that considered to be permanent damage to the crown of the tree.

The role of epicormic leaves must be considered in the analysis of the impact of defoliation on sugar maple even though the function of this foliage is not fully known. The epicormic foliar unit ratio (*E*) in non-defoliated control trees in closed stands was consistently less than 1,

revealing that, under normal conditions, fewer epicormic foliar units are produced in successive years (Table 1). Treated trees had *E* values greatly exceeding those of the control trees and increasing in magnitude with increased defoliation. Among completely defoliated trees, 3 were dead in 1959; 2 trees defoliated in the lower 2/3 and 1 tree defoliated in the upper 2/3 level were dead in 1959. All other trees survived that year.

1960 evaluation. Two years following defoliation, an increase in tissue mortality was evident (Table 2). As a seasonal mean, the completely defoliated trees

Part IV, Table 1. The mean impact in 1959 of each sugar maple defoliation treatment for the combined 1958 closed stands.

Degree and position of defoliation	Number of trees	Live terminal	Epicormic sprouts		Dead	<i>E</i> ¹	Number of trees dead
			Old	New			
Percent of total foliar units							
Complete	35	9.6	1.3	27.0	62.1	20.7	3 ²
Lower 2/3	30	29.5	2.5	16.2	51.8	6.4	2 ³
Upper 2/3	30	23.1	2.6	19.0	55.3	7.4	1 ⁴
Lower 1/3	30	50.3	1.1	10.4	38.2	5.5	0
Upper 1/3	30	50.3	2.1	11.3	36.3	5.5	0
Control	31	82.9	3.3	0.7	13.1	0.2	0

¹ E = Epicormic foliar unit ratio.

² Mortality in 7/21 and 8/11/58 treatments.

³ Mortality in 7/21 and 8/4/58 treatments.

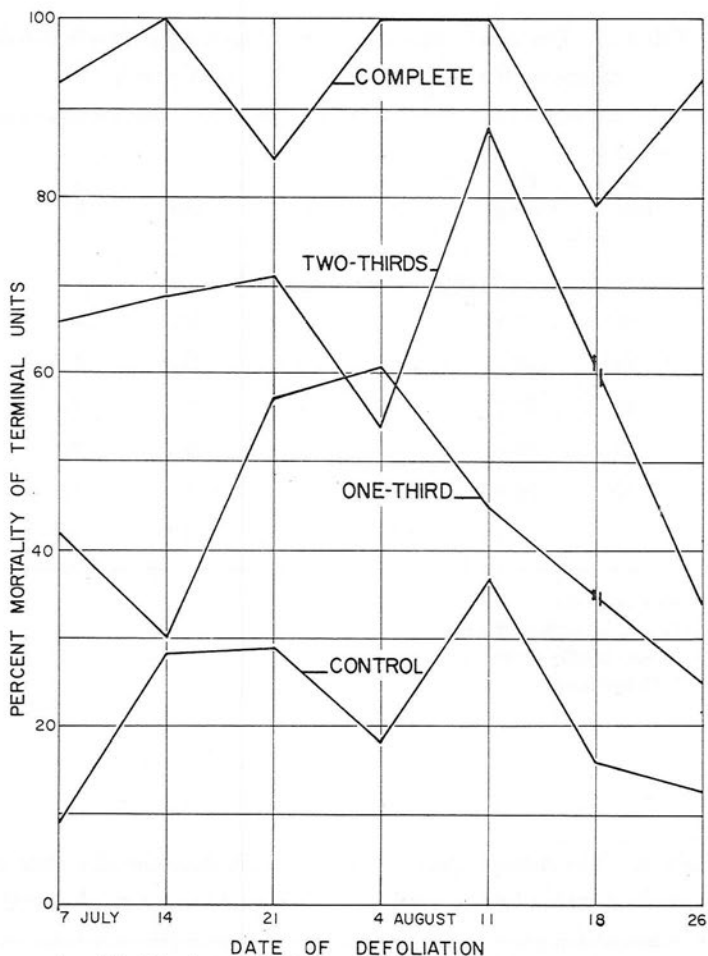
⁴ Mortality in 7/7/58 treatment.

Part IV, Table 2. The mean impact in 1960 of each treatment for trees defoliated by artificial means for the combined 1958 closed sugar maple stand.

Degree and position of defoliation	No. trees	Percent of terminal units as		Percent of 1959 epicormic sprouts surviving in 1960	Mean number of epicormic sprouts per tree per year (of surviving trees)			Number of dead trees
		Living	Dead		1959	1959	1960	
Complete	14	9.9	90.1	26.4	2.8	36.8	1.4	6 ¹
L 2/3	12	44.4	55.6	40.4	1.6	13.8	2.6	1 ²
U 2/3	12	30.6	69.4	46.5	1.3	18.1	5.2	1 ²
L 1/3	12	59.8	40.2	51.4	1.4	8.8	3.0	0
U 1/3	12	51.8	48.2	47.4	1.0	7.9	4.7	0
Control	13	77.8	22.2	100.0	4.2	1.2	2.2	0

¹ Mortality in 7/14, 8/4 and 8/11/58 treatments.

² Mortality in 8/4/58 treatment.



Part IV, Fig. 6. Terminal unit mortality in 1959 resulting from defoliation of closed-stand sugar maple saplings 1 year before.

manifested an increase of twig mortality of more than 25% over the loss of the previous year. Partial treatments and controls evinced an increase of less than 15%. Additional tree mortality was noted in the second year.

The proliferation of epicormic sprouts on defoliated trees was limited to the year following the defoliation. Although the most severely defoliated trees elicited the greatest number of adventitious sprouts, the sprout tissue remaining alive after 1 year was generally rather low; therefore adventitious growth was of questionable survival value. Usually, the percentage of epicormic sprouts surviving the following year was greater where de-

foliation had been less severe. Two years after the initial treatment, the epicormic sprout production was greatly reduced and often was less than that of the controls.

By 1960, all of the completely defoliated trees in 3 treatment weeks in 1958 were dead (Fig. 7). Additional mortality was noted among the trees with 2/3 of the crown removed. As in 1959, no trees died in 1960 among trees defoliated after August 11, 1958.

1960 evaluation of trees treated both in 1958 and in 1959. The terminal twig mortality of sugar maples defoliated on the same date in the same manner for 2 successive years was approximately the

Part IV, Table 3. The mean impact in 1960 of each treatment for trees defoliated by artificial means in 1958 and on the same date in 1959 in closed sugar maple stands.

Degree and position of defoliation	No. trees	Percent of terminal units as		Percent of 1959 epicormic sprouts surviving in 1960	Mean number of epicormic sprouts per tree per year (of surviving trees) before			Number of trees dead
		Living	Dead		1959	1959	1960	
Complete	21	14.6	85.4	10.4	1.4	44.7	2.4	9 ¹
L 2/3	18	43.3	56.7	34.2	2.9	16.2	3.9	0
U 2/3	18	22.7	77.3	21.9	3.4	19.3	4.1	2 ²
L 1/3	18	58.1	41.9	25.7	1.2	13.8	4.2	0
U 1/3	18	59.2	40.8	20.7	2.6	12.3	5.3	0
Control	19	80.7	19.3	85.7	3.5	1.1	2.9	0

¹ Mortality in 7/14, 7/21, 8/4 and 8/11/58 and 59 treatments.

² Mortality in 7/7 and 8/4/58 and 59 treatments.

same in 1960 as in trees defoliated once (Table 2, 3). Statistically, these differences were not significant. This suggests that the initial severe defoliation effected the greatest impact to the trees. A major difference between the once and the twice defoliated trees was the second year survival of sprouts produced after the first defoliation was greatly reduced for twice-defoliated trees. In both defoliation experiments, survival of epicormic sprouts was least for completely defoliated trees and better for partially defoliated trees.

The magnitude of tree death 2 years after the original treatments was similar for trees having either 1 or 2 complete defoliations. Also, mortality was only slightly greater for trees having had 2/3 of the foliage removed twice than those defoliated once to the same degree (Tables 2, 3). No mortality occurred among trees with sectional crown loss to the lower or upper 1/3 treatments and none among the controls.

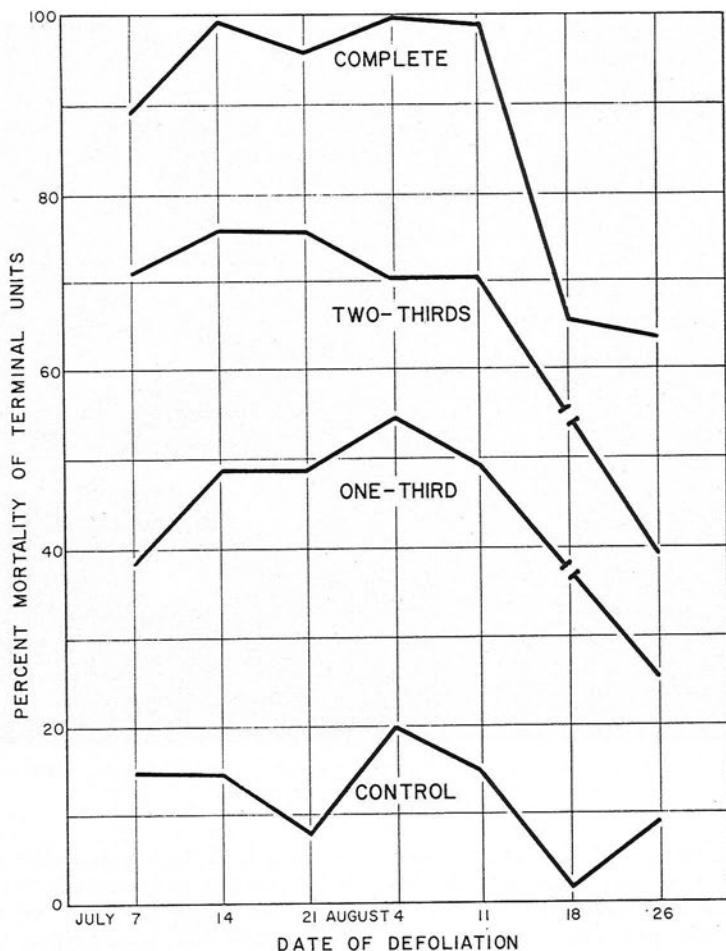
The Impact of 1958 Defoliation in Open Stands

A second growth stand dominated by sugar maple was opened in 1958 by completely defoliating all trees within the plot. The size of the trees was such that all crown classes could be treated to compare with closed stand trees which were predominantly suppressed. One year following treatment, the symptoms of maple blight, including mortality were present. A major difference between the 2 types of stands studied was that the defoliated open stand trees sustained mortality of total foliar units about $\frac{1}{2}$ that of the closed stand trees (Table 4). As with the suppressed tree studies, the number of twigs surviving increased with successively later defoliations. No tree mortality occurred among trees defoliated after August 10. Control tree in this study was located adjacent to the treated open plots and exceeded the *E* ratio value of those

Part IV, Table 4. The mean impact in 1959 caused by complete artificial defoliations of second growth sugar maple in the open-stand condition in 1958.

Date of defoliation	Number of trees	Live terminal	Percent of total units as epicormic sprouts		Dead	<i>E</i> ¹	Number of trees dead
			Old	New			
August 3	97	25.5	5.5	22.3	46.7	4.0	6
August 10	49	26.1	4.8	18.8	50.3	4.0	6
August 16	10	26.5	5.5	23.0	45.0	4.2	0
August 23	7	58.0	4.7	7.2	30.1	1.5	0
Control (Bent)	11	83.2	7.2	3.8	5.8	0.5	0

¹ *E* = Epicormic foliar unit ratio.



Part IV, Fig. 7. Terminal unit mortality resulting from defoliation of closed-stand sugar maple saplings in 1960, 2 years following treatment.

trees growing under normal stand conditions beyond the influence of increased light. All treated trees exceeded the numerical *E* of the control trees.

In 1960, the open stand trees defoliated in 1958 were re-examined. Of a sample of 18 trees defoliated on August 3, 1958, 40.1% of all foliage units were dead and 15.9% of the epicormic sprouts elaborated in 1959 were dead in 1960. The mean number of epicormic sprouts per tree declined from 9.6 in 1959 to 2.6 in 1960. (See Table 4.)

A double-stemmed dominant tree in this plot, with stem diameters of 3 inches

and the stem height of 39 and 38 feet, respectively, for the 2 halves, was bent and the shorter stem was defoliated completely on August 10, 1958. One year later, the treated and untreated portions of this twin tree had respectively: (1) 53.5 and 3.6% of the total units dead, (2) 24.5 and 89.2% of the terminal units alive, (3) 22.0 and 7.2% of the total units present as epicormic sprouts and (4) *E* values of 17.7 and 3.0. The impact of defoliation was a 13-fold increase in unit mortality and a three-fold increase in *E* over the untreated stem. This suggests that adventitious foliage is en-



Part IV, Fig. 8. Epicormic growth and dead terminal units 1 year after the complete defoliation of an open stand tree.

hanced by 2 factors—defoliation or crown destruction (the major action) and increased light availability.

The prolific production of epicormic sprouts in response to defoliation has at least apparent survival value for the tree. This was demonstrated with a 13-foot, open-stand tree, completely stripped in 1958. No epicormic sprouts were present at the time of treatment. One year following treatment, 100% or 63 terminal units (an equivalent to a foliage potential of 252 leaves) were dead on this tree. Complete stripping evoked 31 new luxuriant epicormic sprouts, comprised of 4 to 8 leaves each (Fig. 8). A total of 183 leaves was present or a reduction in leaf numbers of only 27%. The time has been too brief to reveal the true capacity for tissue of epicormic origin to carry the tree through a period of disaster. A preliminary viewpoint is that, under proper conditions of light, vigorous trees can counteract severe defoliation by prolific

production of epicormic shoots from already existing, but normally latent buds.

On the series of trees re-defoliated on the same date 1 year later, 43.5% of the foliage units were dead in 1960. In 1959, prior to re-defoliation, these trees had an average of 11.0 epicormic sprouts per tree, but 1 year later, the mean number per tree had declined to 1.8. 96% of the 1959 sprouts produced were surviving the following year. In principle, but to a lesser degree, crown destruction in open areas follows the same pattern as those growing under a dense canopy. Tree and partial crown mortality occurred and epicormic sprouts were produced in abundance in the growth season immediately following crown disruption. In the second season, sprout production declined to normal.

Eight of the trees originally treated on August 10, 1958 were defoliated again on that date in 1959. The initial treatment had resulted in a reduction of 44.4% of

the foliar units. Prior to the 1958 treatment, a mean of 5.4 adventitious sprouts per tree was determined, while in 1959, this mean was 10.5. In 1960, 1 year after the second complete foliage removal, 38.8% of the units were dead, indicating a slight improvement in crown condition. An average of 2.8 new epicormic sprouts remained per tree, 93.1 of the 1959-produced epicormic sprouts survived.

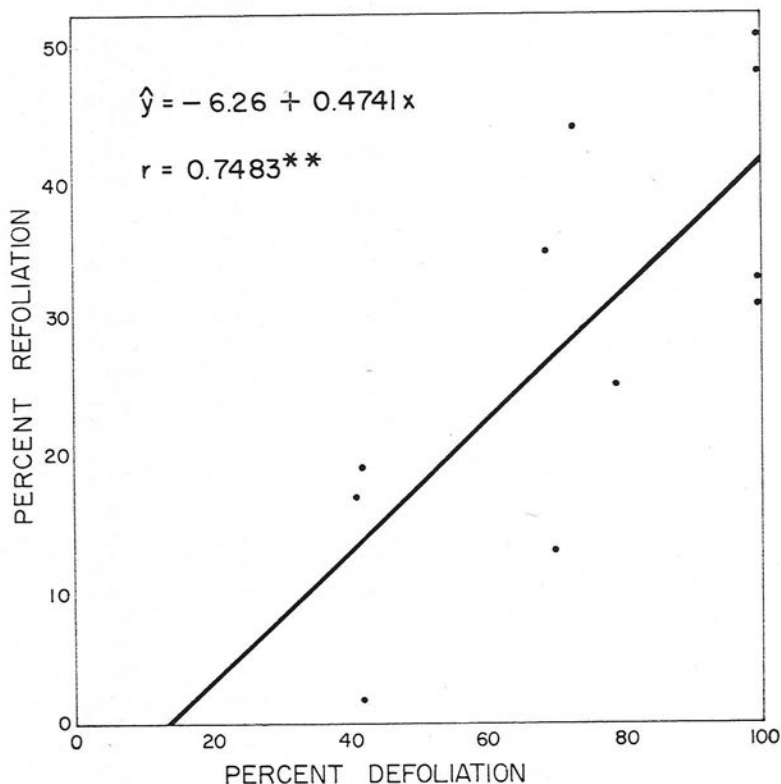
The Impact of 1959 Defoliations in Closed Stands

1959 evaluation. Sugar maples in closed stands defoliated in 1959 were analyzed in the same season after the termination of the growth period and prior to leaf abscission. Refoliation in 1959 was similar in its gross aspects to the effect in 1958, in that the most severe stripping elicited the greatest response (Table 5).

A highly significant correlation exists between the amount of foliage removed and the magnitude of refoliation in the same season (Fig. 9) where $y = 6.26 + 0.474x$ and $r = 0.748^{**}$. Most of the deviation from the expected curve is the result of differences in time of defoliation.

Complete defoliation stimulated 43% of the trees to respond, while lesser treatments evoked responses from 11 to 30%. Of these responding trees, a seasonal mean of 26% normal reflush, 5% epicormic (new or old) reflush and 69% dormancy was exhibited by the complete defoliation series. Of the partial defoliations, the reflush was greater on trees that had the upper crowns treated. In the year of defoliation, the epicormic sprouts represented the smallest type of reflush growth.

The relative numbers of trees that responded to defoliation in the 1959 season



Part IV, Fig. 9. The relationship between defoliation and refoliation in the same season. (100% defoliation points represent weekly means for 5 trees while the partial defoliation data each represent 10 tree weekly means.)

Part IV, Table 5. Analysis of refoliation for 1959 treated closed-stand trees treated at weekly intervals (Evaluated October 15, 1959).

Treatment Date	Estimated foliage defoliation	Actual percent crown defoliation	Percent of foliar units on defoliated branches of responding trees as			
			Reflush	Epicormic sprouts	Dormant	Percent of trees reflushed
6/17	100	100.0	28.1	20.3	51.6	100
	L 2/3	77.2	10.7	0.0	89.3	100
	U 2/3	81.2	41.6	0.7	57.7	100
	L 1/3	—	0	0	100.0	0
	U 1/3	57.9	18.7	0.7	80.6	60
6/23	100	100.0	38.9	11.7	49.4	80
	L 2/3	67.3	22.0	0.0	78.0	100
	U 2/3	71.8	48.0	0.9	51.1	100
	L 1/3	34.6	12.9	1.5	85.6	100
	U 1/3	46.7	19.3	0.0	80.7	80
6/30	100	100.0	28.6	4.3	67.1	100
	L 2/3	68.4	3.2	0.4	96.4	80
	U 2/3	71.3	20.2	2.1	77.7	100
	L 1/3	42.0	2.3	0.0	97.7	40
	U 1/3	42.5	2.7	0.0	97.3	20
7/7	100	100.0	12.8	2.3	84.9	80
	L 2/3	68.6	8.3	0.0	91.7	40
	U 2/3	57.9	4.6	0.0	95.4	20
	L 1/3	40.5	5.9	0.0	94.1	20
	U 1/3	42.7	6.2	0.0	93.8	20
7/14	100	100.0	30.4	0.7	68.9	100
	L 2/3	—	0	0	100.0	0
	U 2/3	73.3	39.8	4.5	55.7	40
	L 1/3	—	0	0	100.0	0
	U 1/3	—	0	0	100.0	0
7/21	100	100.0	5.6	0	94.4	60
	L 2/3	73.1	3.5	0	96.5	20
	U 2/3	75.3	3.0	0	97.0	20
	L 1/3	—	0	0	100.0	0
	U 1/3	—	0	0	100.0	0
7/28 ¹	100	100.0	23.3	0	76.6	80
	L 2/3	62.8	3.1	0	96.9	20
	U 2/3	79.8	12.6	2.3	85.1	40
	L 1/3	—	0	0	100.0	0
	U 1/3	—	0	0	100.0	0
Seasonal ² means	100	100.0	25.9	5.3	68.8	42.9
	L 2/3	69.6	11.8	0.1	88.1	25.7
	L 2/3	74.1	32.9	1.4	65.7	30.0
	L 1/3	36.8	9.5	1.0	89.5	11.4
	U 1/3	49.6	16.0	0.3	83.7	12.9

¹ Treatments after July 28 resulted in no detectable response in the same year.

² Each treatment class represents data from 70 trees.

declined steadily and no reflushing occurred after the July 28 treatment. Among the series in which the lower 2/3 were defoliated, trees from only the first 2 weeks of treatment showed 100% response and trees 1/3 defoliated all responded only for the June 23 lower treatment.

Again, after 1 year, the reflushing terminal and axillary buds were usually dead. Then the epicormic growth became the major foliage type in the area of prior treatment.

Ultimately, the threshold of bud mortality of severe injury and its relation to degree of defoliation must be established. At present, it is possible to rank the impact of treatments by their effect on the basis of reflushing and mortality. Using combined crown levels ranked according to units remaining dormant (least to most) and epicormic sprouting and normal terminal unit reflushing (most to least), the treatments fall into the following order in terms of seasonal means: complete, 2/3 and 1/3 of crown removal. This is the response in the same year. When considering terminal unit mortality and epicormic sprouting after 1 year (from greatest to least), the treatments are ordinated in the same relationship: complete, 2/3 and 1/3 defoliation. This attests again to the significant proportionate relationship between impact and level of defoliation.

The number of reflushing leaves and the length attained in the season of defoliation can be assumed to be an index of the energy output elicited by leaf removal. Combined data for the season in

the closed stand plots demonstrate that the greatest number of leaves reflush on the completely denuded trees (Table 6). The mean length of control leaves was 9.0 cm, while that of the complete defoliation series was 4.2 cm. Both levels of 2/3 stripping yielded mean leaf lengths of 3.5 cm and the upper and lower 1/3 stripping had mean leaf lengths of 3.4 and 2.5 cm respectively. The differences in response between upper and lower investments were not significant.

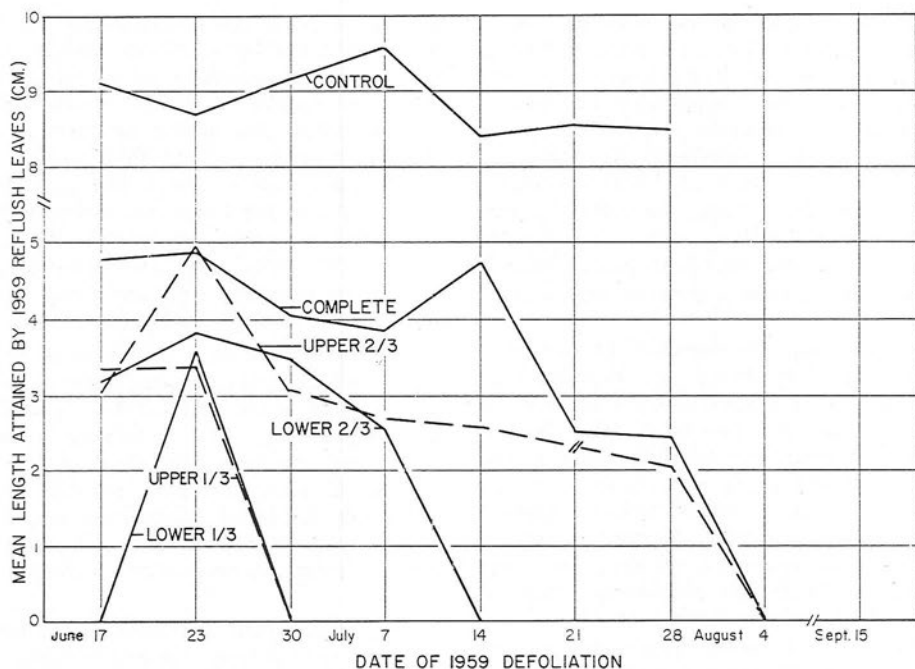
When examined on a weekly basis, re-growth arising from denuded portions of treated trees never attained the normal leaf length (Fig. 10). Following peak leaf growth by trees defoliated on June 23, reflush leaves on trees partially or completely defoliated attained less length progressively to the end of the growing season directly in proportion to the defoliation.

On a time scale, maximum response was observed for trees that had the upper 2/3 or all of the leaves removed. Loss of the lower 2/3 and the upper and lower 1/3 of the foliage complement caused a corresponding reduction in size of leaves produced.

The effect of time of defoliation on the numbers of reflushing leaves is demonstrated graphically in Fig. 11. Reflushing reached a peak as a result of the June 23 complete defoliation treatment; dormancy of buds increased on a time scale inversely to epicormic growth. Each of the remaining levels and degrees of treatment followed the general pattern as

Part IV, Table 6. Mean length of 1959 reflush leaves from closed stand sugar maple saplings defoliated in 1959.

Degree of defoliation	Number of leaves	Mean length (cm)
Complete	276	4.2
Upper 2/3	140	3.5
Lower 2/3	59	3.5
Upper 1/3	70	3.4
Lower 1/3	31	2.5
Control	300	9.0



Part IV, Fig.10. The effect of defoliation intensity and timing on the length of reflush closed stand sugar maple sapling leaves in 1959.

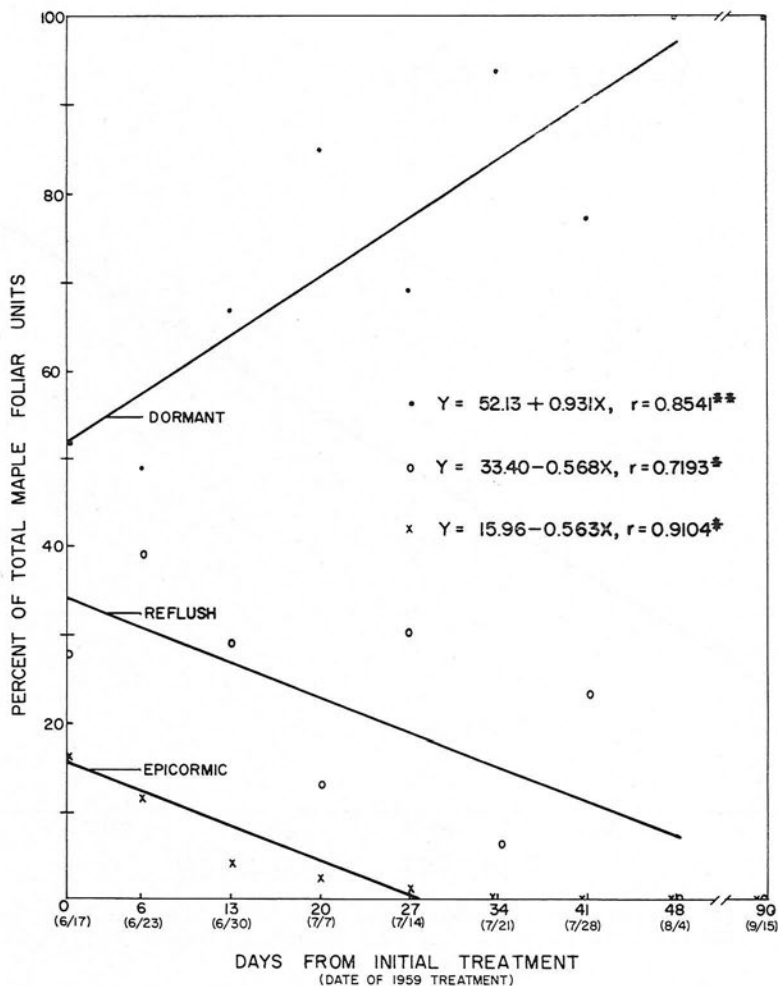
that of the completely defoliated series described above.

Completion of 2 years of the 3 year experiment demonstrated that the most severe defoliation brought about the greatest number of reflushing trees, the greatest number of reflushing foliar units, and greatest leaf lengths in the same season that defoliation occurred. Greatest response in the year of stripping did not result in the best survival the following year. In fact, 1 year after severe denuding, some trees were dead.

1960 evaluation. One year following the treatment, evaluation of the second year's series demonstrated conclusively that 1/3 to complete defoliation had a deleterious effect on sugar maple. The mean percentage of dead terminal units increased in an approximate directly proportionate relationship to the amount of foliage removed (Table 7). Twig mortality, tree mortality and the epicormic sprout ratio were greatest in the completely defoliated series, proportionately less in the partial defoliation series and least in the control groups.

The destruction of equivalent amounts of foliage from 2 crown levels resulted in different responses. Lower crown defoliations produced less twig mortality than upper crown treatments. However, the adventitious sprout production elicited by treatment to the upper portion of the tree was about twice that of the lower. Were epicormic sprouting effective as a survival mechanism, loss of upper crown leaves would be least catastrophic; however, partial crown losses have resulted in tree mortality at both the upper and lower levels.

The magnitude of twig mortality in 1960 of closed stand sugar maple saplings partially to completely defoliated in 1959 was positively and highly significantly related to the relative severity of the defoliation ($y = 16.03 + 0.612x$ and $r = 0.819^{**}$) (Fig. 12). Most of the variation evident on this relationship probably results since mortality (y) is the result of defoliation (x) for a given level at different times throughout the growing

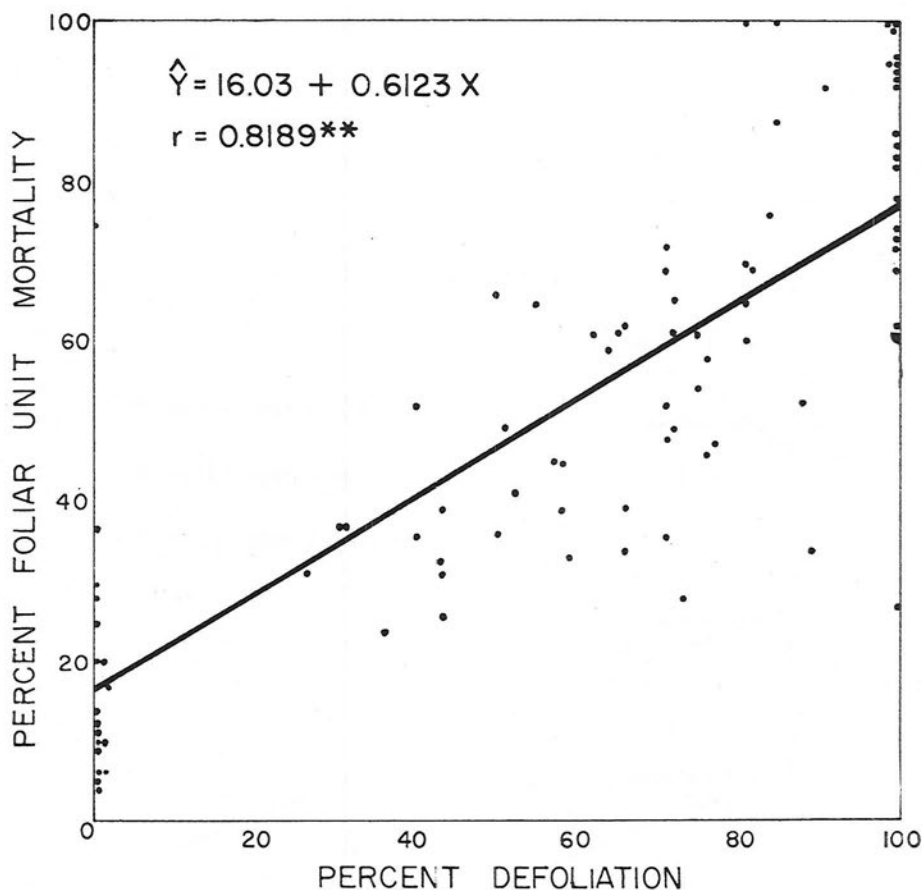


Part IV, Fig. 11. The effect of time of defoliation on reflush foliar unit production by completely defoliated closed stand sugar maple saplings.

season. The amount of refoliation is directly and highly significantly related to the foliar unit mortality the year following defoliation (Fig. 13) where $y = 23.93 + 1.786x$ and $r = 0.818^{**}$.

Complete removal of leaves resulted 1 year later in 92% mortality of units in mid-June, an increase to 100% by August 4 and then a steady decline until, by the end of the growing season, 43% of the potential foliage was lost (Fig.

14). The same trends were manifested by trees having had a part of the foliage destroyed. The expansion of defoliation time, both earlier and later in the season than in 1958, followed by evaluation of defoliated trees, suggests that a *critical period*, that interim during the growth season when the trees are most susceptible to impact caused by destruction of the crown, can now be defined. This critical period for sugar maple is from mid-June through August.



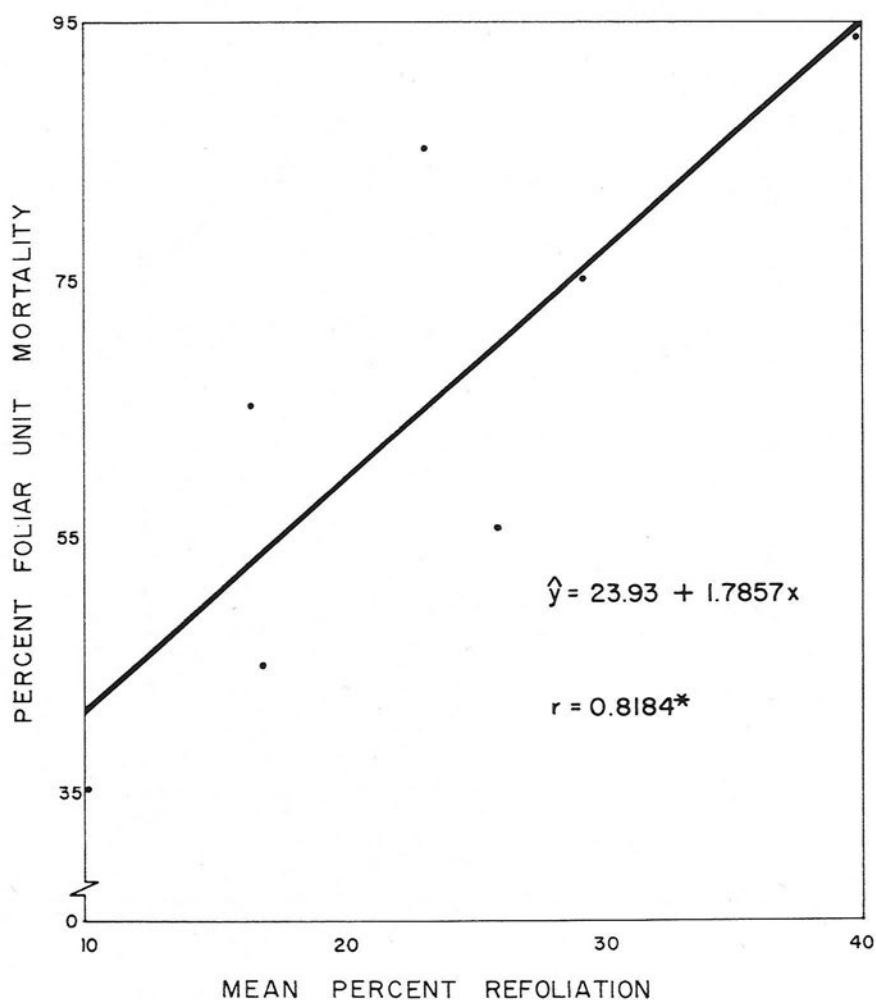
Part IV, Fig. 12. The relationship of artificial defoliation of closed stand sugar maple saplings to the mortality of foliage producing tissue the following year. (Based on 89 experimental 1959 trees.)

The Impact of 1960 Defoliation in Closed Stands

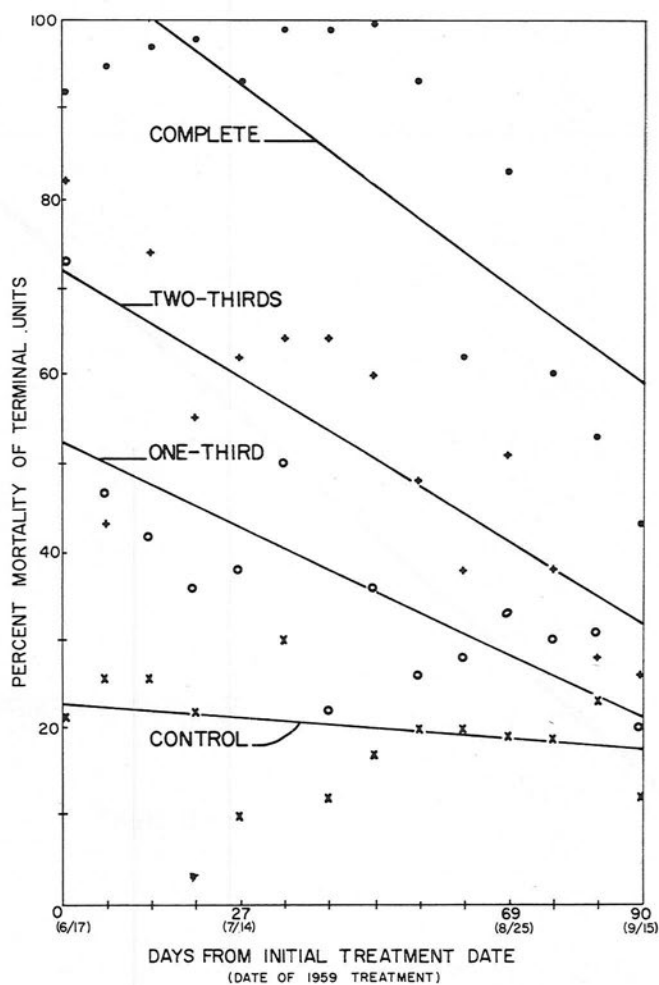
1960 evaluation. In 1960 an 8-level defoliation treatment of closed stand sugar maple saplings was initiated with the first 5 levels applied and timed to correspond to the complete and sectional crown regimes employed in 1958 and 1959. In addition, 1 of 4, 2 of 4 and 3 of 4 of the 4-leaf foliar unit were removed from another series of sugar maple saplings on a similar time schedule.

Trees receiving complete sectional crown defoliation refloshed in the same

season as defoliation in approximately the same relationship as occurred in 1958 and 1959. The great proportion of trees refloshed and the greatest relative tree reflosh on a ranked basis were among those completely defoliated and the least among those that had lost 1/3 of their foliage (Table 8). Early season treatments elicited the greatest response with a gradual decline in refoliation when defoliation was conducted later in the season. Saplings defoliated completely through July 23 refloshed 100%. Reflosh dropped to 20% and no reflosh occurred on trees completely stripped after August



Part IV, Fig. 13. Refoliation response of closed stand sugar maple saplings related to mortality of foliage producing tissue the following year. (The means of 1959 reflush are plotted at the mid-points of 10% size classes and based on a total of 61 trees from the 1959 experiment.)



Part IV, Fig. 14. Terminal unit mortality in 1960 resulting from defoliation of closed-stand sugar maple saplings in 1959:

<i>Treatment</i>	<i>Symbol</i>	<i>b</i>	<i>a</i>	<i>r</i> ¹
Complete	closed circles	-0.795	107.42	0.795
Two-thirds	crosses	-0.445	72.22	0.784
One-third	open circles	-0.344	51.91	0.739
Control	x's	-0.065	22.70	0.335

¹ Tabular $r_{0.5} = .532$, $r_{0.1} = .661$.

Part IV, Table 7. The mean impact in 1960 of each treatment for trees defoliated by artificial means in 1960 for the combined 1959 closed sugar maple stand.

Degree and position of defoliation ¹	Percent of total units as				<i>E</i> ²	Number of trees dead
	Living Terminal	Epicormic Old	New	Dead		
Complete	13.6	1.2	17.0	68.2	14.0	2 ³
L 2/3	48.1	0.8	6.5	44.6	8.1	2 ³
U 2/3	39.4	3.1	11.1	46.4	3.6	0
L 1/3	62.3	1.7	3.5	31.5	2.0	2 ³
U 1/3	56.5	3.9	6.0	33.6	1.5	0
Control (Bent)	75.0	5.1	1.0	18.9	0.2	0
Control (non-bent)	65.6	3.5	0.8	30.1	0.2	0

¹ Each treatment level and control contains 70 trees.

² *E* = Epicormic foliar unit ratio.

³ Mortality at one year in 6/17/59 treatment.

Part IV, Table 8. The estimated response of closed stand sugar maple saplings in 1960 to defoliation treatments by artificial means conducted in the same year.

Treatment ¹	Percent of trees responding	Estimated mean Ranked Reflush of responding trees (0-5 possible)
Complete	58.6	3.5
Lower 2/3	31.4	1.4
Upper 2/3	42.9	2.1
Lower 1/3	7.1	1.4
Upper 1/3	30.0	1.3

¹ 70 trees per treatment.

10. The response to partial sectional crown defoliation also declined as the season progressed, roughly in proportion and ranked reflush, to the severity of treatment.

Sugar maple saplings receiving the 1 to 3 of 4 foliar unit removal reflushed very little when treatment was applied early in the season and no reflush was observed after July 13.

1961 evaluation. One year following the defoliation of the sugar maple saplings on plots established in 1960, two types of evaluation were conducted. First, because of budgetary economics, the actual foliar unit impact was determined for the June 9 and June 23 treatment weeks. In the second type of evaluation the proportion

of trees that succumbed and the mean percent of dead crown on living trees was estimated for the weekly treatments.

On the 2 treatment week plots evaluated in detail, the impact of foliar unit mortality again reflected the severity of sectional crown defoliation. Completely defoliated trees sustained the greatest foliar unit mortality and tree mortality with the 2/3 and 1/3 crown removal saplings sustaining lesser degrees of injury (Table 9).

Uniform, entire crown, partial defoliation effect was ordinated with the greatest impact occurring on the 3 of 4 leaf foliar unit defoliation. However, the magnitude of twig mortality in these treatments was, with only one exception, well

Part IV, Table 9. A partial evaluation in 1961 of closed stand sugar maple saplings defoliated by artificial means in 1960.

Treatment	Percent of total units as					Number of trees dead
	Living Terminal	Epicormic		Dead	<i>E</i>	
	Old	New				
June 9, 1960						
Complete ¹	5.5	0.8	9.3	84.4	11.8	3
L 2/3	35.7	6.9	16.2	41.2	2.4	0
U 2/3	38.5	0.3	8.3	52.9	25.0	0
L 1/3	33.6	5.6	10.9	49.9	1.9	0
U 1/3	57.8	0.3	3.6	38.3	12.0	0
1 of 4	67.1	6.2	0.0	26.7	0.0	0
2 of 4	73.3	4.1	1.8	20.8	0.4	0
3 of 4	62.1	2.7	2.5	32.7	0.9	0
Control	76.4	3.2	0.4	20.0	0.1	0
(Bent)						
Control	79.0	0.7	0.0	20.3	0.0	0
(non-bent)						
June 23, 1960						
Complete	3.1	0.0	12.3	84.6	48 ²	2
L 2/3	38.0	0.0	9.8	52.2	47 ²	0
U 2/3	21.0	8.3	20.3	50.4	2.4	0
L 1/3	45.9	0.2	9.4	44.5	41.0	0
U 1/3	49.5	5.3	12.5	32.7	2.3	0
1 of 4	74.5	6.4	1.4	17.7	0.2	0
2 of 4	60.5	3.0	5.3	31.2	1.8	0
3 of 4	37.1	2.8	5.4	54.7	1.9	0
Control	81.9	1.0	0.0	17.1	0.0	0
(Bent)						
Control	81.1	1.5	0.0	17.4	0.0	0
(non-bent)						

¹ Each treatment and control contains 5 trees.

² Absolute number of sprouts, there being no previous sprouts.

below that caused by complete sectional crown treatment at the 1/3 level.

The elaboration of adventitious tissue, expressed in the *E* ratio was greatest on the most severely sectionally defoliated saplings and least on those less severely treated. On the uniform crown defoliated saplings adventitious tissue development was greatest on the most severely treated saplings (3 of 4=0.9 and 1.9) and least on the least severely treated tree (1 of 4=0.0 and 0.2) on June 9 and June 23, respectively. This lower 1-year twig mortality and epicormic sprouting demonstrated by the uniform defoliation is

doubtless related to the meager reflushing in the year of defoliation.

Examination of the seasonal mean percentage of crown mortality data collected 1 year later (Table 10) illustrates that, as in 1958 and 1959, the most severe sectional crown defoliation caused the greatest twig mortality. On saplings completely stripped, 58.6% of the twigs succumbed and from 28.1 to 21.7% for the lower 2/3 to upper 1/3 crown defoliation treatments. Uniform partial defoliation was reflected in the approximate magnitude equal to the twig mortality of the non-defoliated control saplings.

Part IV, Table 10. The mean estimated foliar impact in 1961 of closed stand sugar maple saplings defoliated by artificial means in 1960 by date of treatment.

Date of 1960 treatment	Mean Percent of Crown Dead								Treatment control	Untreated control
	Complete	<i>Two-thirds</i>		<i>One-third</i>		<i>1 of 4</i>	<i>2 of 4</i>	<i>3 of 4</i>		
		Lower	Upper	Lower	Upper					
June 9	85.0 ¹	53.1	44.2	38.4	52.9	28.5	21.7	33.6	20.7	20.5
15	86.7 ²	50.0	43.3	20.0	20.0	20.0	20.0	16.7	16.7	16.7
23	84.6 ²	52.2	55.0	44.6	34.6	18.9	32.1	56.3	17.3	17.6
29	70.0	23.3	40.0	26.7	23.3	13.3	20.0	23.3	16.7	20.0
July 6	76.7 ²	30.0	16.7	23.3	16.7	20.0	30.0	10.0	16.7	30.0
13	76.7 ²	43.3	33.3	30.0	16.7	16.7	20.0	6.7	3.3	20.0
20	63.3	36.7	23.3	23.3	23.3	20.0	20.0	16.7	23.3	20.0
27	53.3	26.7	33.3	30.0	23.3	20.0	26.7	16.7	16.7	30.0
August 3	60.0	23.3	26.7	23.3	16.7	20.0	30.0	23.3	16.7	26.7
10	36.7	20.0	13.3	33.3	23.3	16.7	16.7	16.7	26.7	26.7
17	36.7	23.3	16.7	36.7	26.7	20.0	23.3	30.0	13.3	50.0 ²
24	66.7	20.0	50.0 ³	16.7	33.3 ³	40.0 ³	16.7	33.3	16.7	16.7
31	46.7	16.7	20.0	33.3	23.3	23.3	33.3	40.0	16.7	20.0
September 7	30.0	23.3	13.3	16.7	13.3	10.0	13.3	13.3	10.0	20.0
Season Mean	58.6	28.1	27.5	26.1	21.7	20.0	22.5	20.6	16.1	24.7

¹ 60% trees dead.

² 40% trees dead.

³ 20% trees dead.

On a seasonal basis, again, the severity of reaction declined rapidly after August 3 on the completely defoliated saplings and after June 23 on the partial sectional crown treatments. Partial uniform crown defoliation had no demonstrable impact in relation to time of treatment.

An Evaluation of Mechanical Defoliation of Closed Stand Sugar Maple Saplings in Door and Iron Counties

In 1959 artificial defoliation plots were established in sugar maple stands in Door and Iron Counties, Wisconsin to obtain data in areas remote from the maple blight center in Florence County. Treatment regimes including sectional crown defoliation similar to those employed earlier were established on July 28 and 29, and evaluation was conducted in 1960.

No sapling mortality occurred on either area treated and the twig mortality was ordinated in proportion to the severity of defoliation (Table 11). Also, the *E* ratios were ordinated in the same sequence indicating that the response to defoliation in these areas remote from the maple blight center was consistent with the findings previously reported.

An Evaluation of Impact of Defoliation on Selected Hardwoods

Because sugar maple sustained severe injury from partial to complete defoliation at various times during the growing season, an investigation of the impact of defoliation of selected hardwoods in the open growing northern forests was initiated. Sapling yellow birch, basswood, and ironwood were completely defoliated in

Part IV, Table 11. Evaluations in 1960 of closed stand sugar maple saplings defoliated in 1959 in Iron County and in 1960 and 1961 for Door County, Wisconsin.

Percent of total units as: ¹								
Area	Treatment	Number of trees	Living Terminal	Epicormic		Dead	<i>E</i> ¹	Percent mean dead crown (1961) ²
				Old	New			
Door County	Complete	10	18.9	0.7	20.0	60.4	28.6	56.7 ³
	L 2/3	5	41.1	2.1	9.4	47.4	4.4	30.0
	U 2/3	5	44.0	4.9	17.2	33.9	3.5	10.0
	L 1/3	5	65.5	1.5	4.1	28.9	2.7	13.3
	U 1/3	5	65.3	0.8	7.7	26.2	10.3	13.3
	Control (Bent)	5	83.3	1.6	0.0	15.1	0.0	6.7
	Control (non-bent)	5	72.0	0.8	1.1	26.1	1.2	13.3
Iron County	Complete	10	13.3	1.2	12.1	73.4	9.8	—
	L 2/3	5	28.6	1.6	4.8	65.0	3.0	—
	U 2/3	5	45.2	4.1	8.0	42.7	1.9	—
	L 1/3	5	63.7	5.0	5.6	25.7	1.1	—
	U 1/3 ⁴	5	—	—	—	—	—	—
	Control (Bent)	5	79.2	0.6	0.0	20.2	0.0	—
	Control (non-bent)	5	81.8	2.6	1.2	14.4	0.5	—

¹ Data based on actual foliar unit tabulations in 1960.

² Data based on estimated foliar impact in 1961.

³ Three trees had dead crowns, but had elaborated epicormic sprouts on the basal 1/3 of the bole.

⁴ No data available.

Florence County on August 3, 1959, and the impact evaluated later the same season and the following year.

Yellow birch was the most susceptible among the hardwoods defoliated. By the thirtieth day following treatment, reflushing leaves had appeared (Fig. 15). However, 1 year later, 3 of the 10 treated trees had died (Table 12) and 86% of the survivors had all of their leaves originating from new epicormic sprout tissue.

Ironwood also reflushed in the season of defoliation; these leaves were smaller and fewer in number than normal. Two of the ironwood trees were dead in 1960, and 65.4% of the leaves on the survivors were of epicormic origin.

Basswood was least affected by the mechanical defoliations. Leaves of reflush were present in about equal numbers and size within 30 days after treatment (Fig. 16). None of the treated trees succumbed and they appeared normal 1 year later.

These observations corroborate the findings of Barter and Cameron (1955) who reported differential host susceptibility to defoliation by the forest tent cater-

pillar. Paper birch sustained greater loss in radial increment from less severe defoliation than aspen.

The Relationship of Insect Defoliation to Maple Blight

In 1955, 1956 and 1957, partial to complete defoliation of sugar maple was caused by 3 insect species. The 2 solitary leaf-rolling tortricids, *S. acerivorana* and *A. chalybeana*, persisted in their active feeding stages from mid-May to mid-August. In late June, a third insect, the maple webworm, *T. asperatella*, appeared and by mid-July reached a peak in numbers and defoliating potential. The webworms are colonial and as many as 224 larvae may inhabit each rolled leaf provided by one of the leaf rolling species. The colonial behavior gives rise to an aggregated distribution and feeding patterns that result in a rapid defoliation of large sections of the crown. This *en masse* feeding behavior is analogous to the sectional crown defoliation experiments. The leaf rollers are solitary feeders and tend more



Part IV, Fig. 15. The reflush of second growth yellow birch 30 days following complete defoliation.

Part IV, Table 12. The 1960 response of selected hardwood species to complete defoliation by artificial means in 1959.

Species	Number of trees	Mean Height (feet)	Percent of buds as		Number of trees dead
			Living	Dead	
Yellow birch					
Treatment	10	11.2	4.9	95.1	3
Control	3	9.8	83.3	16.7	0
Basswood					
Treatment	10	10.4	67.8	32.2	0
Control	5	10.5	76.2	23.8	0
Ironwood					
Treatment	10	10.6	5.1	94.9	2
Control	4	12.5	81.3	18.7	0

towards a random distribution. Consequently, this feeding pattern is analogous to the uniform crown defoliation where a portion of each terminal unit was removed throughout the crown. Growth loss occurred with both sorts of mechanical defoliation. However, the damage induced by the sectional technique was the greatest. The most devastating defoliation pressure by this complex of insects falls specifically at a time during the critical period when susceptibility is the highest.

Although complete defoliation was probably the exception and occurred only in localized pockets, major defoliation was widespread. Webworms seek the more exposed portions of the tree crown as well as the more exposed parts of the stand. Here they attain their maximum population and developmental growth. Thus, the colonies are usually found in the upper and outer portions of the tree crown where leaf consumption inflicts the greatest impact.

Timing, site, species attacked and severity of insect depredations all are critical factors in terms of growth impact, but epiphytotic populations of defoliating insects during the months of June, July and August, under any conditions, can be expected to be catastrophic to susceptible species of trees and to cause, in sugar maple, the condition known as maple blight.

Maple Blight and the Influence of Defoliation by the Saddled Prominent

An opportunity to evaluate the impact of defoliation by a different species of insect was afforded in Door and Kewaunee Counties, Wisconsin. The lepidopterous insect, the saddled prominent, *Heterocampa guttivitta* (Wlkr.), has the larval stage represented by one of the larger caterpillars, attaining a length of nearly 2 inches. In July of 1955, 1956 and 1957, saddled prominent larvae stripped, either completely or to a major extent, the foliage of sugar maple, beech, ash and ironwood in certain areas (Anon. 1954; Anon. 1957; and Anon. 1958). In 1959, within 2 to 4 years following the epiphytotic, these areas in both counties exhibited all the symptoms of classical maple blight in Florence County (Figs. 17, 18 and 19).

The Door County stand evaluated in this study was dominated by sugar maple and ironwood and had about an equal admixture of beech, basswood and ash (Table 13). Living trees were recorded as not affected, or affected; in the latter case they displayed one or more of the symptoms of maple blight. Many trees had the major complement of foliage represented as epicormic sprouts (Fig. 18).



Part IV, Fig. 16. The reflush of second growth basswood 30 days following complete defoliation.

Wilting, dieback and mortality were evident. Most of the maple, ironwood, beech, and ash were affected (Table 14). Of all the trees present, 22.5% were dead, while the mortality of all saplings was 12.2%. Prior to the blight, 185 trees and 588 saplings were present per acre. A pre-blight basal area of 78.8 square feet per acre was reduced 22.7% following the blight. The basal area of sugar maple was reduced 40.5%.

Similar conditions were observed in a Kewaunee County hardwood forest where the saddled prominent was in outbreak during the same period (Fig. 19).

The mode of action of defoliation in terms of growth impact is now explicable.

While it is true that the 1 year mortality of foliage-producing tissues correlates with the relative severity and time of crown destruction the previous year, this action is actually indirect. The amount of observable refoliation in the same year also is directly related to the severity and time of defoliation in that year. The buds giving rise to this refoliating tissue usually were latent buds, and those that yield leaves for the following year. That trees apparently do not reflush in the same year does not mean that growth or differentiation is not occurring in terminal meristematic regions. It is entirely possible that growth and expansion of buds occur and would go undetected except for histologi-



Above: Part IV, Fig. 17. Typical maple blight following defoliation of sugar maple by *Hemerocampa guttivitta* in Door County, Wisconsin.

Below: Part IV, Fig. 18. Adventitious growth of sugar maple in blighted area of Door County, Wisconsin.





Part IV, Fig. 19. Kewaunee County, Wisconsin maple blight area with recent history of severe defoliation by *Hemerocampa guttivitta*.

Part IV, Table 13. Characterization of a mixed northern hardwood stand defoliated by the saddled prominent (Door County, Wisconsin).

Species	Relative Density				Relative Dominance		Relative Importance ⁴		Continuum Index ⁴	
	Trees ¹		Saplings ²		Trees ³		Pre-	Post-	Pre-	Post-
	Pre-	Post-	Pre-	Post-	Pre-	Post-				
Sugar maple	44.2	31.4	28.9	21.6	53.9	41.5	49.1	36.4	1472.0	1093.5
Ironwood	23.4	26.7	26.7	28.7	9.1	10.7	16.2	18.7	438.8	504.9
Basswood	11.7	15.1	9.9	11.3	11.7	15.1	11.7	15.1	280.8	362.4
White ash	9.0	11.6	11.3	12.9	10.4	13.4	9.7	12.5	232.8	300.0
Beech	8.1	10.5	16.7	18.7	9.1	11.8	8.6	11.2	258.0	334.5
Black oak	2.7	3.5	0.3	0.3	3.0	3.9	2.9	3.7	21.2	27.8
Red oak	0.9	1.2	0.3	0.3	2.8	3.6	1.8	2.4	33.0	43.2
Others ⁵	—	—	5.9	6.2	—	—	—	—	—	—
							Total		2736.6	2666.3

¹ Based on 185 trees per acre pre-blight; 143 trees per acre post-blight.

² Based on 588 saplings per acre pre-blight; 517 saplings per acre post-blight.

³ Based on 78.8 sq.ft. per acre pre-blight; 61.0 sq.ft per acre post-blight.

⁴ Based on tree attributes only.

⁵ Includes balsam fir, black cherry, big tooth aspen and hemlock.

Part IV, Table 14. The mortality and vigor status of tree species in a Door County, Wisconsin stand.

Species	Trees			Saplings		
	Percent of species as Dead	Percent of living trees as Affected	Vigorous	Percent of species as Dead	Percent of saplings as Affected	Vigorous
Sugar maple	44.9	100.0	0.0	34.3	83.6	16.4
Ironwood	11.5	100.0	0.0	5.3	78.6	21.4
Beech	0.0	88.9	11.1	1.7	65.5	34.5
White Ash	0.0	90.0	10.0	0.0	5.0	95.0
Others	0.0	29.4	70.6	3.4	5.4	94.6
Stand	22.5	83.7	16.3	12.2	54.5	45.5

cal examination. Tree mortality the following year also is related positively to refo-
liation. The mode of action follows a se-
quence of defoliation, refo-
liation and mortality. Defoliation elicits refo-
liation which reduces or exhausts the bud supply
too late in the season for new bud pro-

duction. Mortality of foliage producing
tissue occurs the following year and if
tissue mortality exceeds the threshold of
the physiological system to compensate
for disruption of the conductive tissue
and reduction or loss of food production,
then the tree dies.

Summary

Experimental mechanical defoliation elicited the following responses in sugar maple: (1) in the current year—reflushing, slight epicormic sprouting and major apparent bud dormancy, (2) 1 year following defoliation—slight normal flushing, major epicormic sprout production, extensive woody tissue and bud mortality giving rise to dieback symptoms, wilting and occasional tree mortality, and (3) 2 years following defoliation—almost no further epicormic sprouting but additional wilting, either a further increase in tissue mortality or tree mortality or an improvement of the crown. Both tissue and tree mortality are positively and significantly correlated to the severity of defoliation.

A *critical period* is defined within which sugar maple is highly susceptible to defoliation. This period (mid-June through August) was concomitant with the maximum feeding activity of the major defoliating insects that were epiphytotic prior to the appearance of maple blight. The symptoms produced by insect defolia-

tion and mechanical defoliation induced within the critical period are identical with those of maple blight.

The mode of action of maple blight is described as a phenomenon whereby defoliation elicits refo-
liation and this refo-
liation exhausts or reduces the supply of buds and subsequent tissue and tree mortality may occur. Yellow birch and ironwood also are highly susceptible to damage caused by defoliation.

Epiphytotics of the saddled prominent resulting in partial to complete defoliation of sugar maple and other hardwoods in Door and Kewaunee Counties were followed by maple blight.

Thus, defoliation of sugar maple by insects at varying crown levels and degrees is the primary factor involved in the genesis of maple blight. Death and twig mortality of sugar maples may occur whenever insect epiphytotics destroy large amounts of foliage during the critical period.

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Part V. Ecological Factors Associated with Maple Blight

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PART V.

Ecological Factors Associated With Maple Blight

Darroll D. Skilling¹

A. An Environmental Study of the Maple Blight Area:

Introduction

AN ECOLOGICAL STUDY was initiated during the summer of 1958 to determine the roles forest stand characteristics and environmental factors might play in the cause, spread, and intensification of maple blight. A survey of the

affected area was undertaken to determine the possible relationship of environmental factors to maple blight. The results of the survey suggested possible causes of blight that were tested in a healthy stand of sugar maple, *Acer saccharum* Marsh.

Methods and Materials

Sampling Procedure

Preliminary examinations of the maple blight areas on the forest holdings of Calumet and Hecla, Inc., near Goodman, Wisconsin, revealed that severe tree mortality was confined to small pockets in

which almost all trees were affected. Around these loci, a scattering of dead and dying trees extended out into the adjacent stands for a considerable distance. To obtain a representative sample of conditions throughout the blight area, a series of 1/5-acre plots was established

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at 5-chain intervals along transects that extended from the healthy portion of the stand into the area of heavy tree mortality. Altogether, 113 plots were established within the maple blight area.

Soil samples were collected from 4 general locations within the blight area. At each location, 6 soil pits were dug within a 1/5-acre area. Soil samples were collected from the A₂, B, and C horizon in each pit. The 6 samples for each horizon were then combined for analysis.

All trees were tallied by diameter and species, and each sugar maple was classi-

fied according to the severity of blight symptoms. Four categories were defined: Class 1, healthy trees, Class 2, trees with less than 1/3 of the crown showing blight symptoms, Class 3, trees with over 1/3 of the crown affected, and Class 4, trees dead from blight. Class 2 trees were omitted in the analysis, as it was difficult to determine whether these always were affected by maple blight. In addition, information was collected on several environmental factors that influence the growth and vigor of a forest tree. These factors included stand characteristics, past history of the area, topography, climate, and soil.

Observations and Experimental Results

Stand Characteristics

An inverse relationship was demonstrated between stand density (as measured here, stand density refers to square feet of basal area per acre in all trees 2.6 inches dbh and larger) and the percentage of maple trees with blight symptoms (Fig. 1). The high density plots had 22% of the maple with blight symptoms; low density plots had 70% of the sugar maple with maple blight. Moreover, stands with the lowest number of trees per acre (all species) also had the highest percentage of maple with blight (Fig. 2).

The incidence of maple blight present was related to the species composition on the plots. The percentage of sugar maple with blight symptoms increased as the proportion of basal area in sugar maple increased (Fig. 3).

No relationship was evident between the number of trees with maple blight and tree size-class distribution. As much blight was present in sapling and pole stands as in sawtimber stands. No relationship was found between the number of trees with blight and tree age.

In 1948, prior to the appearance of maple blight symptoms, twenty 1/4-acre growth plots had been established in this area by Calumet and Hecla Incorporated foresters. Tree vigor had been recorded

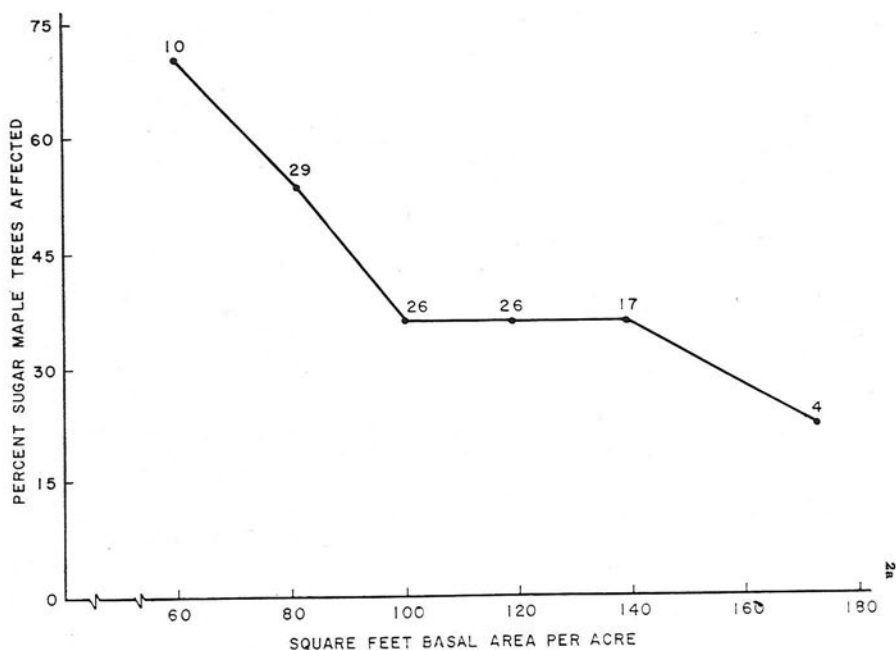
for each tree, according to the tree classification developed by Region 9, U.S. Forest Service (1943). A re-examination of these trees in 1958 showed no correlation between tree vigor in 1948 and severity of maple blight symptoms in 1958.

A sample of 34 trees with maple blight symptoms was examined to determine whether a general decline in growth rate had preceded the development of blight symptoms. Measurement of annual growth rings at 1 foot above ground height for the period 1930 to 1958 showed no growth reduction until the trees began to show symptoms of maple blight.

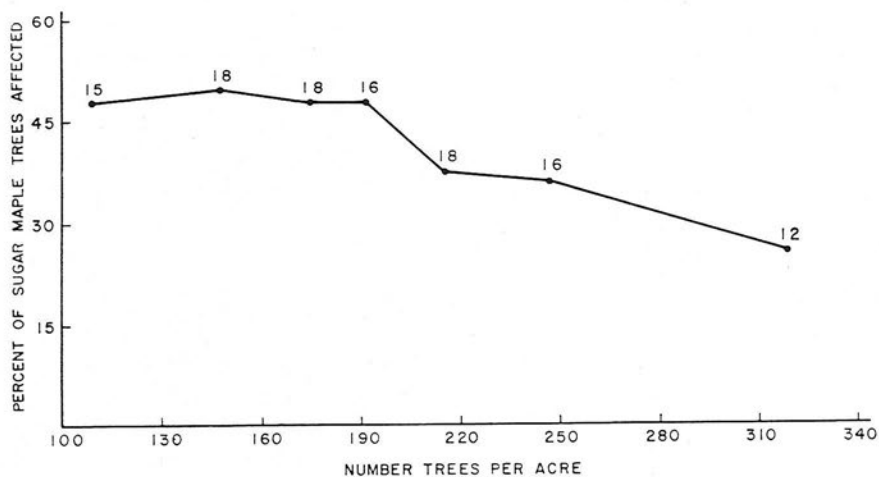
Areas with severe maple blight had above-normal amounts of ground vegetation as compared to nonblighted areas. The increased amount of ground vegetation in the blighted stands probably reflected both insect defoliation and mortality of sugar maple, which permitted an increase in the amount of light. No single plant species, however, was found only in association with blight areas.

Past History

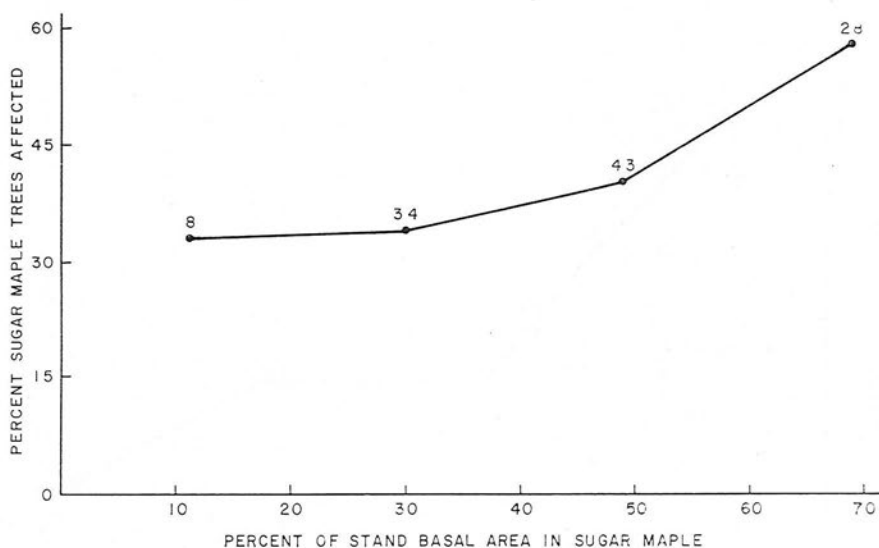
No relationship was found between maple blight and preblight cutting practices. Heavy maple blight mortality was present in some areas where no cut had been made for at least 20 years. Individual blighted trees did not show an un-



Part V, Fig. 1. The relationship of maple blight to stand density. Basal area includes all trees 2.6 inches d.b.h. and larger. Numbers on the curve refer to the number of 1/5-acre plots measured at each point.



Part V, Fig. 2. The relationship of maple blight to total number of trees per acre 2.6 inches d.b.h. and larger. Numbers on the curve refer to the number of 1/5-acre plots measured at each point.



Part V, Fig. 3. The relationship between maple blight and species composition. Numbers on curve refer to 1/5-acre plots measured at each point.

usual amount of logging damage. No evidence was found that windthrow, sunscald, sleet damage, or fire had played any role in the development of maple blight.

The only factor consistently related to the blight condition was the past insect infestations. The sugar maple of this area had previously sustained severe insect defoliation as discussed in Part II.

Topography

The elevation of an individual plot in relation to the surrounding area was recorded to determine if this was related in any way to incidence of blight. Approximately 65% of the sugar maples on upper flat areas had severe maple blight as compared to 40% of the maple on the slopes and lowland areas. No relationship was found between the percentage of trees with blight symptoms and plot aspect or degree of slope.

Climatic Factors

Weather records were obtained from three stations located 13 miles northeast,

9 miles southeast, and 9 miles west of the maple blight area for 1953 to 1958. In the 10-month period prior to the severe tree mortality in 1957, precipitation at these stations was 8.3 inches below normal.

The weather records did not indicate the occurrence of an unusually early frost during the fall of 1956 or 1957. The first killing frost in 1956 was on September 19 when 26° F. was recorded. In 1957 the first below-freezing temperature was 31° F. on September 23.

Soil Factors

In general, the blight area is composed of Iron River and Goodman silt loams, which are normally good hardwood soils. Comparison of the results of this soil analysis with those from other northern hardwood sites showed no severe deficiency of available soil nutrients including trace elements for the growth of sugar maple (Table 1). In addition, the large size and rapid growth of sugar maple on this area in the past was a further indication that soil fertility was not a critical factor in the development of maple blight.

Part V, Table 1. Analysis of soils from areas affected by maple blight¹

Sample area	Soil horizon	Soil pH	Cation exch. cap.	Exchangeable				Total N	Avail P ₂ O ₅	B	Cu	Zn	Soil texture		
				K	Ca	Mg	Mn						Sand	Silt	Clay
			<i>Mq/100 g</i>	<i>Ppm</i>	<i>Mq/100 g</i>	<i>Ppm</i>		<i>Percent</i>	<i>Ppm</i>	<i>Ppm</i>	<i>Ppm</i>	<i>Ppm</i>	<i>Percent</i>		
1	A ₂	4.7	10.5	53	2.60	0.50	13.10	0.088	37.0	0.79	3.0	5.8	24.4	68.6	7.0
	B	4.9	15.6	35	1.15	.28	1.15	.080	67.0	.68	3.0	1.3			
2	A ₂	4.2	11.7	50	1.95	.37	30.40	.091	48.5	.66	1.5	3.0			
	B	4.9	20.0	36	3.90	.38	1.50	.097	136.5	.71	1.5	1.5			
	C	4.9	7.5	35	1.35	.54	.63	.012	42.5	.79	3.0	.8	29.0	61.8	9.2
3	A ₂	4.4	10.3	58	2.00	.52	2.50	.083	54.0	.66	1.0	2.0			
	B	4.6		50	.85	.21	.85	.078	51.5	.99	1.5	1.0			
	C	4.8		26	.35	.12	.75	.045	15.5	.85	1.5	.8			
4	A ₂	4.7		46	2.50	.75	11.80	.078	30.5		1.5	1.7			
	B	5.0		26	1.60	.33	1.40	.058	101.0		2.5	1.3			
	C	5.1		41	.95	.30		.026	49.5		3.0	1.1			

¹ Soils analysis by Soils Department, University of Wisconsin.

Summary and Discussion

The incidence of maple blight was related to several factors including stand density, stand species composition, a past history of severe insect defoliation, and plot elevation in relation to the surrounding area. In addition, prior to the maple blight mortality of 1957, precipitation in the blight area was below normal.

Preliminary defoliation studies in 1958 by Houston (1961) and Giese (1960) showed that artificial defoliation could produce symptoms on sugar maple saplings that were identical to maple blight symptoms. This was good evidence that past insect defoliation was an important factor in the development of the maple blight complex and also served to explain the relationship between the incidence of maple blight and stand density and species composition. Thus areas with a low

stand density and a high percentage of sugar maple were the most favorable areas for the development of an insect epiphytotic (Giese, 1960). These were the areas which also showed the highest incidence of maple blight.

The question now was raised: Did the below-normal precipitation in this area contribute in any manner to the severity of the maple blight complex? Approximately 15% more maples showed blight symptoms on upper flat areas as compared to maples growing on slopes and lowland areas. The upper flat areas were drier in terms of soil moisture. The possibility existed that trees growing on the drier areas might be less vigorous and therefore more susceptible to injury from insect attack.

B. The Effect of Reduced Soil Moisture and Artificial Defoliation on the Development of Maple Blight Symptoms:

Introduction

The results of the initial survey in the Florence County blight area indicated certain problems on which more intensive work should be conducted. One of these

was the effect of below-normal precipitation and insect defoliation on the development of maple blight symptoms.

Methods and Materials

The study was conducted on the Argonne Experimental Forest, outside of and 50 miles west of the Florence County maple blight area. In 1959 when this study was established, maple blight symptoms were not evident in this area. The forest stand was predominantly sugar maple

about 35 years old. Other species included balsam fir, *Abies balsamea* (L.) Mill., red maple, *Acer rubrum* L., yellow birch, *Betula alleghaniensis* Britton, eastern hemlock, *Tsuga canadensis* (L.) Carr., and black cherry, *Prunus serotina* Ehrh.

The upper soil layer was a loesslike cap of silts 12 to 24 inches thick. Under this was a discontinuous layer of sandy loam glacial till ranging in thickness from a trace to over 3 feet. The material underlying this was an outwash plain, consisting of medium and coarse sands containing from 2 to 25% of gravels. The soils that developed from this material were well-drained podzols with a fragipan at depths of 14 to 26 inches. The soil would be classified as Stambough silt loam, although the fragipan was more strongly expressed than normal. The subsurface water table was about 10 feet below the surface. Soil pH, measured at several points and in different soil horizons, ranged from 4.5 to 5.5²

The 20 sample trees selected for this study were sugar maples that averaged 5.2 inches in diameter at breast height and 33 feet in height. All were vigorous with no evidence of maple blight, and all were in the dominant crown class receiving full sunlight.

To reduce soil moisture, a trench approximately 20 inches wide and 3 feet deep was dug around each tree 15 feet from the bole. This was to prevent lateral movement of soil moisture and to eliminate any possible effects of root grafts with other trees. The treatments (assigned at random) and the number of trees receiving each treatment are shown in Table 2.

To reduce the amount of precipitation reaching the root systems of the trees, moisture-intercept platforms were constructed

similar to those used by Cope-land (1955). These consisted of 10 wedge-shaped wooden frames fastened together around the base of the tree about 2 feet above the ground. The platforms were covered with a sturdy polyethylene material that carried the moisture into the trench. During the winter months snow and ice that collected on the platforms were removed. For each of the trees scheduled to receive 50% of normal precipitation, alternate frames were left uncovered (Figs. 4 and 5).

The trees were defoliated by removing the leaves by hand. A tractor-mounted ladder (Fig. 6), which could be positioned at any point in the crown of the tree, was used to reach the leaves and also to record branch growth (Skilling, 1960). On those trees receiving a 50% defoliation, 50% of the leaves were removed from each branch throughout the total crown.

To prevent the time of defoliation from masking the effects of soil moisture reduction and degree of defoliation, the defoliation schedule was arranged so that half of the trees in each treatment were defoliated during the first part of the normal insect defoliation period and half were done during the last part of the period.

The moisture-intercept platforms were completed in June 1959, and the trees were defoliated twice—once during August 8 to 17, 1960, and once during August 7-11 in 1961. These defoliation periods corresponded approximately with the season of

² Credit for the soil description is given to William A. Wertz, Soil Scientist, Forest Service, U.S. Department of Agriculture.

Part V, Table 2. Soil moisture reduction and artificial defoliation study:
Treatments applied and number of trees assigned to each treatment.

Atmospheric precipitation received (percent of normal)	Number of trees receiving		
	No defoliation	50-percent defoliation	100-percent defoliation
0	2	2	2
50	2	2	2
100	4	0	4



Above: Part V, Fig. 4. Moisture-intercept platform showing details of framework construction and encircling trench.

Below: Part V, Fig. 5. Moisture-intercept platform for 100 % moisture reduction.





Part V, Fig. 6. Tractor-mounted ladder used for hand defoliation and terminal bud investigations.

the year when insect defoliation by the webworm, *Tetralopha asperatella* (Clem.), occurred on the Goodman maple blight area in 1955, 1956, and 1957 (Giese, 1960).

Annual measurements were taken of diameter and height growth. Branch growth and bud mortality were determined by annually measuring 10 tagged branches located at random throughout the crown of each tree. Temperature, relative humidity, and precipitation were recorded within the study area throughout the growing season to determine moisture received and time of first fall frost. Soil moisture information was collected for each sample tree throughout the growing season by the gravimetric method (Lull and Reinhart, 1955) (Fig. 7).

In addition, each tree was photographed in color and in black and white each year

at permanent photo stations to determine general changes throughout the crowns.

At the completion of the 1961 growing season, rootlets were taken from each defoliation treatment to determine the effect of defoliation on mortality of the fine feeder roots. The 3 trees sampled had 100% intercept platforms. The five 6-inch-square soil and root samples from each tree were taken from the 6- to 12-inch soil layer. The rootlets were then carefully washed out, and a subsample of 10 root sections was selected at random from each sample. The root sections were observed under a dissecting scope, and each root tip was classified into 1 of 4 types. These were: white (those tips in the most active state of growth), brown (living but not in active growth), swollen nodules (similar to the brown tips but swollen at the ends), and dead root tips.



Part V, Fig. 7. Soil moisture measurements were taken through trapdoors in the intercept platforms.

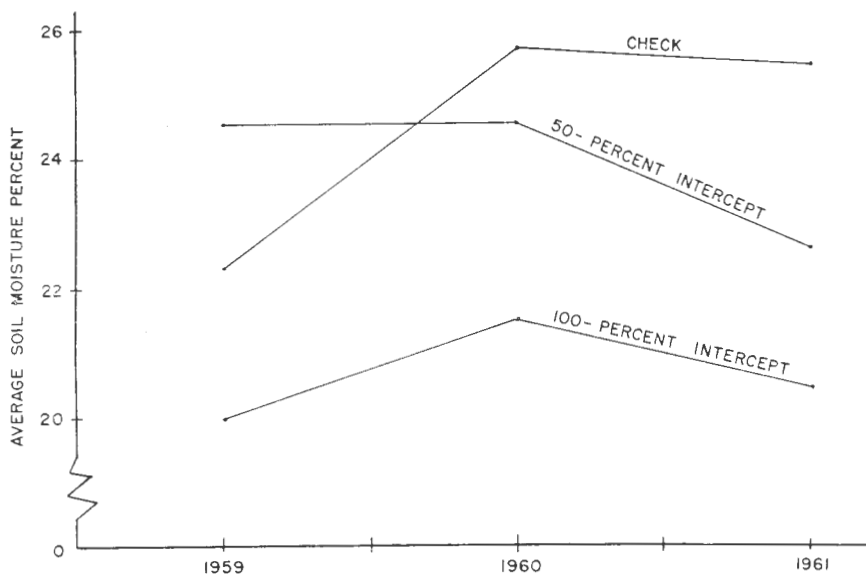
Observations and Experimental Results

The reduction in soil moisture during the growing seasons that resulted from the intercept platforms is shown in Fig. 8. The 0- to 12-inch soil layer contained over 95% of the fine feeder roots and was therefore the critical moisture area. A greater difference in soil moisture had been expected as a result of the intercept platforms. Evidently a subsurface recharge prevented this. A few sugar maple roots were found near the subsurface water table. These roots, however, were only a small fraction of the total root system. The differences in soil moisture that developed in the area containing most of the feeder roots were in the range that would result naturally from a period of below-normal precipitation.

About 20 to 25 days following the 1960 defoliation, certain trees began to reflush. This reflush was related to 2 factors. The first was the severity of de-

foliation. Evidently the 50% defoliation was not sufficient to stimulate growth as none of these trees showed any reflush during the late summer or fall. The trees completely defoliated did reflush, however; and the degree of reflush was related to the time of defoliation. Three trees that were 100% defoliated on August 10 and 11 developed a new crop of leaves approximately $1/3$ their normal size. But only an occasional branch reflushed on the trees completely defoliated between August 15 and 17.

Branches that reflushed did not have sufficient time to develop mature leaves and buds before the normal fall frosts. On September 26, 1960, when temperatures dropped to the low 20's in the open areas and to 27° to 28° F. under the closed canopy, these succulent leaves and partially formed buds were killed. This was the primary reason for the branch dieback



Part V, Fig. 8. Changes in the average soil moisture percent in the 0- to 12-inch soil layer from June to August 1959, 1960 and 1961 due to moisture-intercept platforms.

among the trees during the spring of 1961.

Soil moisture deficiency, coupled with artificial defoliation, had an adverse effect on 1961 terminal branch growth throughout the tree crown, and the effect was additive (Fig. 9). Of the 2 factors, however, defoliation had the greatest effect on branch growth. The growth reduction was uniform throughout the tree crowns.

Dieback of the terminal branches throughout the crown also was related to both soil moisture deficiency and artificial defoliation. Here, again, the effects were cumulative with defoliation showing up as the greatest cause of terminal dieback (Fig. 10).

Following the dieback in the fall of 1960, many sprouts developed from dormant buds closer to the main stem of the tree during the spring of 1961. In many cases, however, these sprouts wilted about the middle of July. This sprout development was very similar to that observed in the Florence County maple blight area during the summer of 1958 (Fig. 11).

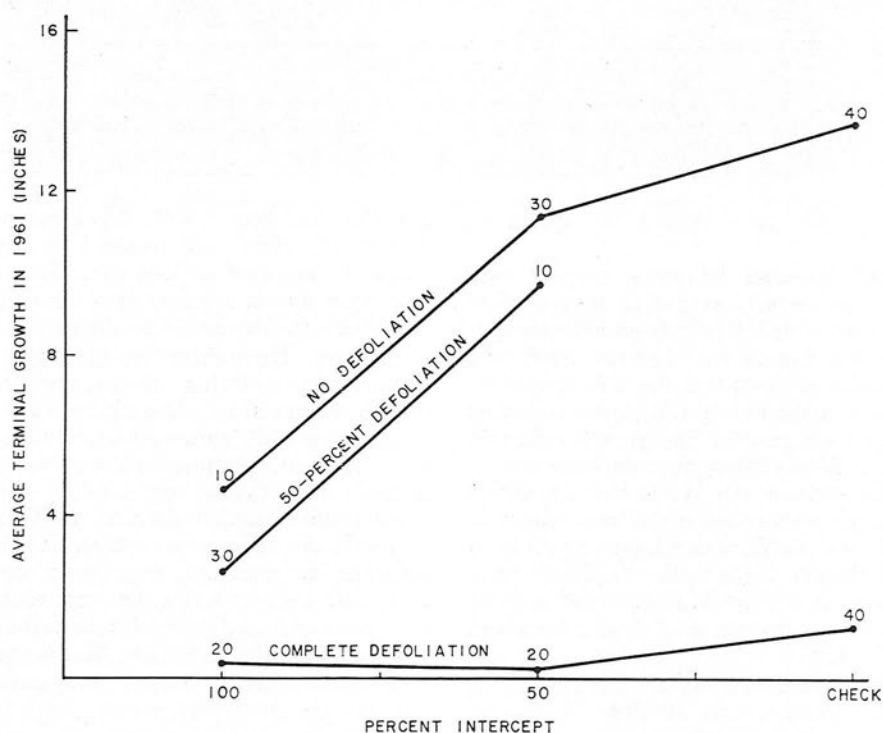
The earliest mortality of treated trees was observed in the spring of 1961. One

tree that had been 100% defoliated on August 10, 1960, and received no precipitation, was dead in June 1961. Several other trees showed severe dieback throughout their crowns, and this dieback was progressive. Throughout the 1961 growing season, branches throughout the crowns continued to wilt and die. At the close of the 1961 growing season, 2 trees were dead and 6 more had such severe dieback that it was very unlikely they could survive another defoliation. These 8 trees had all received 1 complete defoliation the previous year. Both mortality and dieback were again most severe on those trees that received both defoliation and moisture reduction. The 6 trees with severe dieback in 1961 were defoliated for the second time on August 7-11, 1961. In June 1962, 3 of these trees were dead and the other 3 had only a few branches with leaves present.

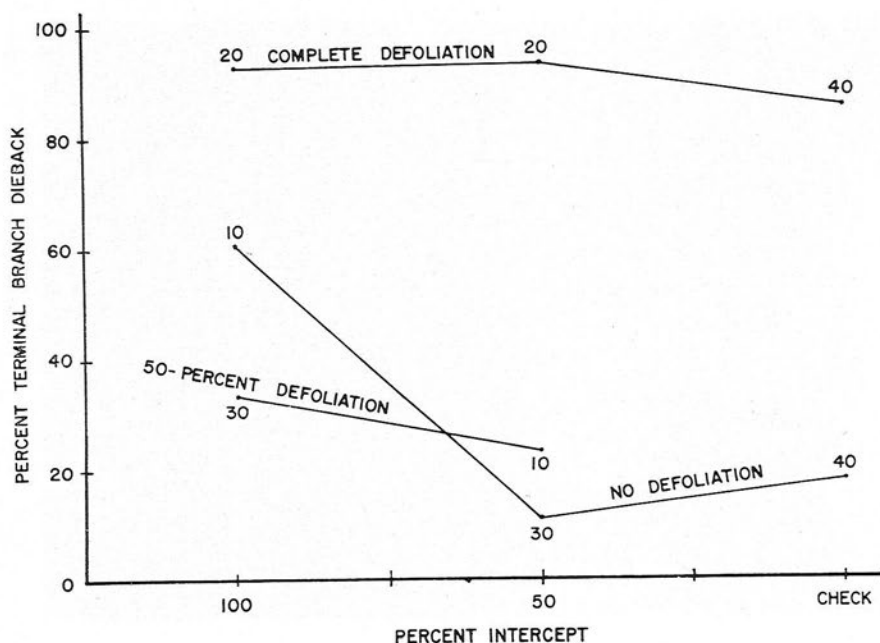
Up to August 1961, defoliation had not affected the condition of the fine feeder roots (Table 3). In fact, more dead root tips were present in the root samples from the nondefoliated trees than from the defoliated trees.

Part V, Table 3. Effect of defoliation on sugar maple rootlets from 3 sample trees, all 100% covered by moisture-intercept platforms.

Percent of artificial defoliation	Condition of root tips								Total
	White		Brown		Nodules		Dead		
	No.	Percent	No.	Percent	No.	Percent	No.	Percent	
100	666	34.6	407	21.1	464	24.1	388	20.2	1,925
50	596	28.2	404	19.1	418	19.7	699	33.0	2,117
Check	678	23.9	623	21.9	757	26.7	782	27.5	2,840



Part V, Fig. 9. The effect of soil moisture reduction and artificial defoliation on 1961 terminal branch growth. Numbers on curve refer to terminal branches measured at each point.



Part V, Fig. 10. Terminal branch dieback, 1961, following soil moisture reduction and artificial defoliation. Numbers refer to terminal branches measured at each point.

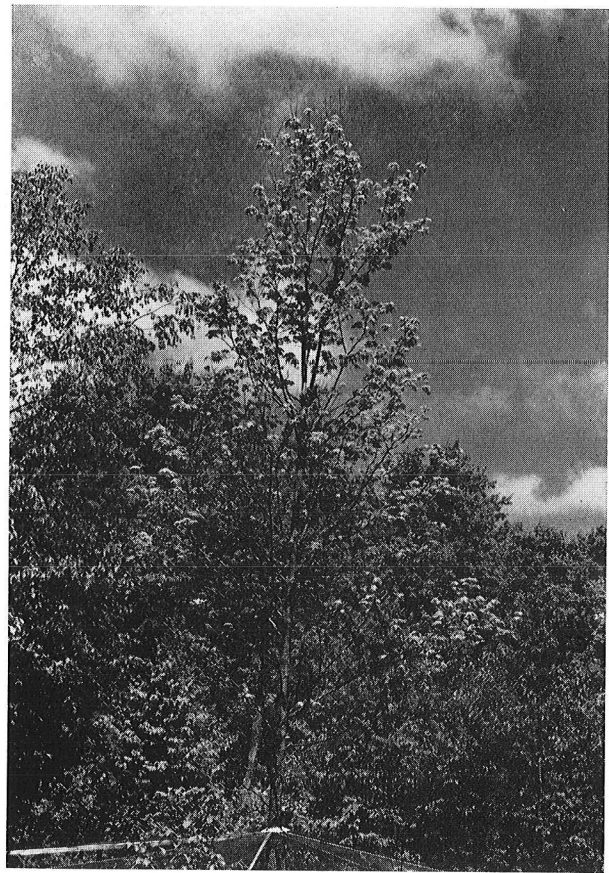
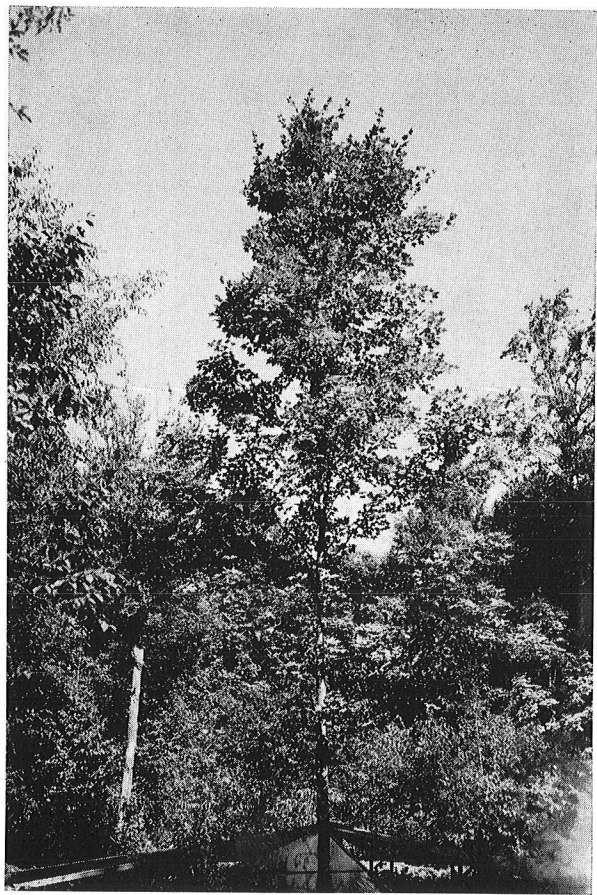
Summary and Discussion

This experiment was an outgrowth of several defoliation studies and an environmental survey within the maple blight area. The results of these studies had indicated that insect defoliation and sub-normal precipitation might be factors causing maple blight.

Healthy, pole-size sugar maple received various degrees of soil moisture reduction and artificial defoliation.

The complete syndrome of maple blight was reproduced by these artificial methods. Artificial defoliation had the greatest effect on the development of maple blight symptoms. Soil moisture reduction, however, served to increase the effects of defoliation in terms of growth reduction, branch dieback, and tree mortality.

Defoliation of sugar maple in mid-August in northern Wisconsin is critical. Sufficient time is available for the defoliated branches to reflush, but not enough of the growing season remains for these branches to form mature buds for the following season. As a result, the undeveloped, succulent buds are killed by normal fall frosts, and branch dieback results. When this condition develops throughout the crown, tree mortality is imminent. Although complete defoliation of pole-size trees for 1 year will cause some mortality, complete defoliation for 2 consecutive years during mid-August will result in very severe stand mortality comparable to that observed on the Florence County maple blight area.



Part V, Fig. 11. *Left*, sample tree receiving 50% soil moisture reduction. Photo taken on August 10, 1959, before defoliation. *Right*, same tree following, a 100% defoliation on August 10, 1960. Photo taken on June 14, 1961.

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