EFFECTS OF SPRUCE BUDWORM-CAUSED DEFOLIATION ON THE GROWTH OF BALSAM FIR: EXPERIMENTAL DESIGN AND METHODOLOGY

by

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ABSTRACT

A detailed study of the relationship between defoliation by the spruce budworm (Choristoneura fumiferana (Clem.)) and growth loss of balsam fir (Abies balsamea (L.) Mill.) trees on the Cape Breton Highlands, Nova Scotia is described. Methodology includes the maintenance of control plots adjacent to defoliated plots by closely-controlled, annual spraying of insecticide; detailed, non-destructive, annual estimation of defoliation on all age classes of foliage on branches throughout the crown of sample trees; non-destructive estimation of foliage biomass based on relationships between weight and needle and shoot dimensions; and determination of current annual volume increment and radial growth by stem analysis. Also included in the study are an assessment of the importance of backfeeding to growth loss, examination of the rate and amount of recovery of growth which can be expected if protection (insecticide spraying) follows several years of defoliation, study of the nutritional and physiological changes in needles after partial defoliation, and monitoring the attack of secondary insects and diseases on defoliated trees. Data are presented on the number of branches and discs per tree required to estimate defoliation and current annual volume increment to a given level of precision. Other results of the study will be reported after the current budworm outbreak collapses.

RESUME

Description d'une étude détaillée sur le rapport existant entre la défoliation causée par la tordeuse des bourgeons de l'épinette (Choristoneura fumiferana (Clem.)) et le ralentissement de la croissance du sapin baumier (Abies balsamea (L.) Mill.) dans les hautes terres de l'île du Cap-Breton, en Nouvelle-Ecosse. La méthodologie comprend l'entretien de placettes témoins voisines de placettes ravagées, au moyen d'une pulvérisation annuelle d'inseciticide, étroitement contrôlée, l'estimation détaillée et sans destruction de la défoliation de toutes les classes d'âge sur les branches de la cime d'arbres échantillons, l'estimation sans destruction de la biomasse du feuillage, basée sur les rapports entre le poids et les dimensions des aiguilles et des pousses, et la détermination de l'accroissement courant annuel en volume et en diamètre par l'analyse de la tige. Cette même étude comprend aussi une évaluation de l'importance de la destruction du feuillage des années antérieures pour le ralentissement de la croissance, un examen de la vitesse et de l'ampleur de la reprise de la croissance auxquelles on peut s'attendre si la protection (épandage d'insecticide) suit une défoliation de plusieurs années, une étude des modifications tropiques et physiologique survenues dans les aiguilles par suite d'une défoliation partielle, et la surveillance de l'attaque d'insectes et de maladies secondaires sur les arbres défoliés. On y présente aussi des données sur le nombre de branches et de disques par arbre qui sont nécessaires pour estimer la défoliation et l'accroissement courant annuel jusqu'à un certain degré de précision. D'autres résultats de cette étude feront l'objet d'un rapport après la fin de la présente infestation.

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INTRODUCTION

Epidemic population levels of the spruce budworm (Choristoneura fumiferana (Clem.)) have resulted in severe defoliation of host tree species over much of eastern North America. Most of the information available on the impact of budworm outbreaks deals with the mortality of trees caused by defoliation; this subject was reviewed by MacLean (1980). The loss of wood production by trees suffering non-fatal defoliation is a less visible but extremely important impact, particularly in view of the timber supply deficits emerging in New Brunswick, Nova Scotia, and other regions (Reed and Associates Ltd. 1978). Few data presently exist to quantify the loss of wood production by trees and stands resulting from varying degrees of defoliation, and yet, it is clear that these data are urgently needed by forest managers to predict accurately wood production and to allocate harvesting for a sustained yield.

Past studies of effects of defoliation on growth of balsam fir (Abies balsamea (L.) Mill.) trees have generally lacked detail. These studies were reviewed by MacLean (1981). They often considered only growth loss at breast height, and attempted to relate this to some gross measure of defoliation (e.g., a light-moderate-severe scale). In general, results showed a loss of 50 to 75% of the radial increment after several years of severe defoliation, with a time lag of 2 to 5 years between the initial defoliation and the first growth loss observed at breast height. However, data from a recent study by Piene (1980) have shown that substantial growth losses may occur much earlier than this in the upper part of the stem. A small reduction in volume increment was evident during the first year of defoliation, and severe defoliation for 2 years, with a loss of two age classes of needles, resulted in about a 50% reduction in current volume growth.

This paper describes the experimental design and methodology of a detailed study of the relationship between defoliation and growth loss of balsam fir on the Cape Breton Highlands, Nova Scotia. There was a need for more detailed knowledge of the amount and temporal sequence of defoliation of individual trees, that could be related to growth data derived from stem analysis. There was also a need for data on the actual biomass of foliage by age class remaining on the tree, rather than just defoliation data, because tree growth is related to the foliage left on the tree, not to the proportion that was removed. Age class of foliage was recognized as being important because Clark (1961) showed that both balsam fir and white spruce (Picea glauca (Moench) Voss) needles decline in their photosynthetic capacity as they age and thus contribute less to tree growth. We wished also to assess the importance of backfeeding (removal of more than the current age class of needles), to follow nutritional and physiological changes in needles after partial defoliation, and to monitor the attack of secondary insects and decays on the defoliated trees. Results of the study will be reported after the budworm outbreak collapses.

DESCRIPTION OF THE STUDY AREA

The study area is in Victoria County, Nova Scotia, at an elevation of approximately 400 m (Fig. 1). It is within the Cape Breton Highland District of the Gaspé - Cape Breton Ecoregion (Loucks 1959-60). The climate is humid and temperate, with a mean annual temperature and precipitation of about 6°C and 125 cm,

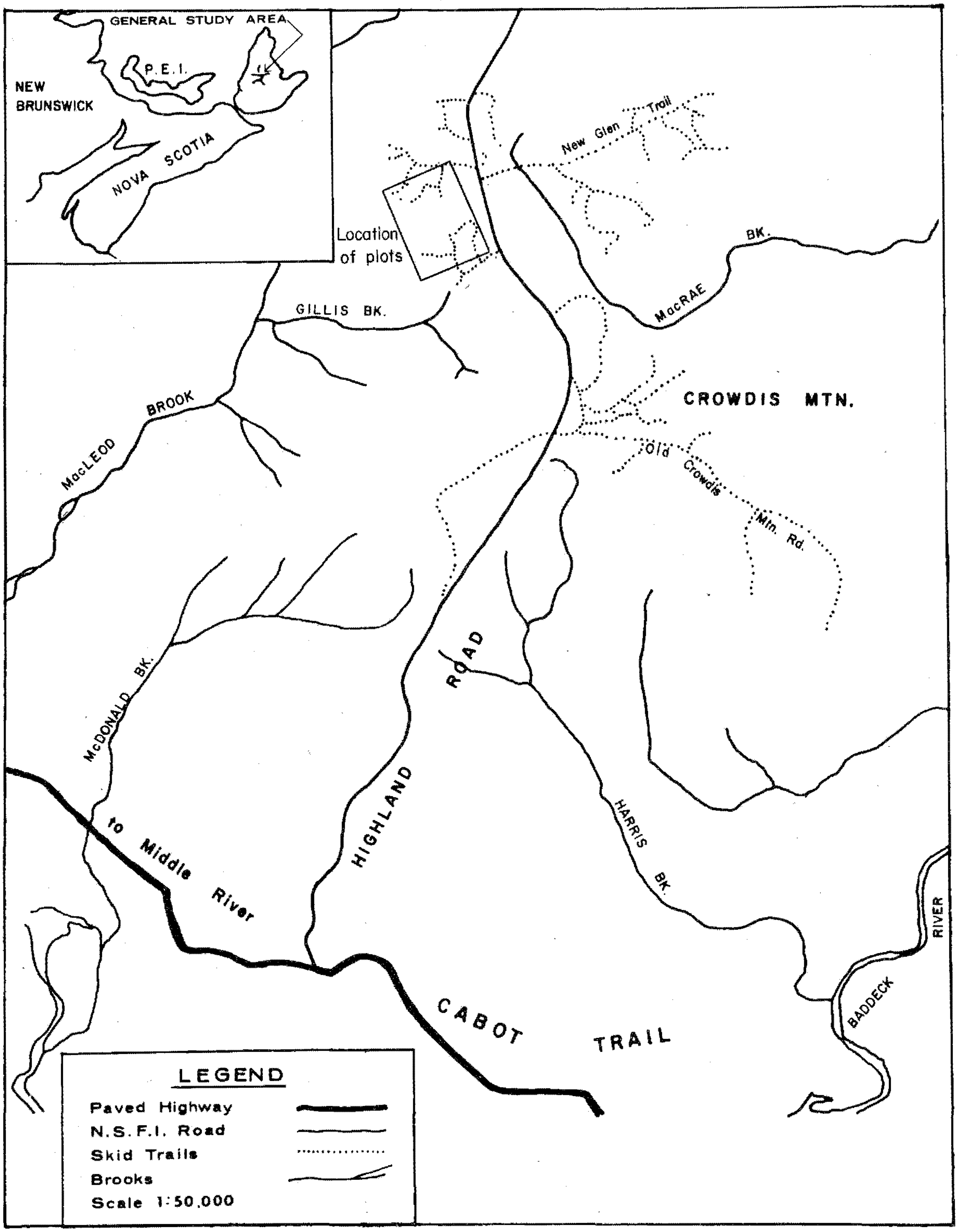

Fig. 1. Location of the general study area and the experimental plots on the Cape Breton Highlands.

respectively. Before the clear-cut in the mid 1950's, the Crowdis Mountain area was covered with an almost pure balsam fir forest, 60 to 80 years old, of average height about 13 m, and with scattered white spruce, white birch (*Betula papyrifera* Marsh.), yellow birch (*Betula alleghaniensis* Britton), and red maple (*Acer rubrum* L.). In most locations, dense stands of balsam fir became established after the clear-cut. In 1971, several of these stands were operationally spaced to about 2.4 x 2.4 m (8 x 8 ft).

The ground vegetation in the spaced and unspaced stands is characterized by the mosses *Pleurozium schreberi* (BSG.) Mitt., *Dicranum* spp., and *Hylocomium splendens* (Hedw.) BSG. Important herbs in the unspaced stands include *Cornus canadensis* L. and *Oxalis montana* Raf., and, in addition, in the spaced stands *Maianthemum canadense* Desf., *Linnaea borealis* L., *Coptis groenlandica* (Oeder) Hult., *Clintonia borealis* (Ait.) Raf., *Gaultheria hispidula* (L.) Muhl. and *Aralia nudicaulis* L. are present. For a more detailed description of the vegetation see Piene (1981).

In 1973, a spruce budworm outbreak started on the northwest coast of the Cape Breton Highlands (Kettela 1973)[1] and devastated large areas of forest. By 1976, it had reached the 25-year-old spaced stands located in the Crowdis Mountain area. Those stands were being studied to determine the growth response to spacing (Piene 1981), and it was decided to initiate a study on the effects of defoliation on growth of these same stands.

EXPERIMENTAL DESIGN

This study incorporates methodology designed to overcome the shortcomings of several earlier studies.

(1) The study was begun in the first year of budworm feeding; failure to be sure of the initial year of feeding, or starting a study after several years of unmeasured defoliation, has been a problem in the past.

(2) We wanted to establish undefoliated, check plots in the immediate area of the defoliated plots, so that growth of defoliated and undefoliated trees could be directly compared. This was accomplished by intensive, closely-controlled, annual spraying of insecticide in the control plots.

(3) We carried out a detailed, non-destructive, assessment of defoliation on the same trees in the plot each year. Thus growth of the trees would not be disturbed by removal of branches for defoliation or insect population level sampling, and yet, an accurate record of defoliation each year on each tree could be maintained. A record of tree growth is maintained in the annual rings; this can be measured at the end of the outbreak.

(4) Defoliation was measured not only for the current age class of needles on the sample trees, but for all age classes, each year. Thus, increases in defoliation of older age classes of needles in successive years could be attributed to backfeeding.

This is the first study of effects of budworm defoliation on balsam fir growth that has detailed records of annual defoliation throughout the crown of sample trees, and the first designed to consider backfeeding. To our knowledge, the only other study which directly compared growth in defoliated and protected plots was a much less detailed study by Batzer (1973).

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1 Kettela, E.G. 1973. Aerial spraying against the spruce budworm in 1973 and a forecast of conditions in the Maritimes Region in 1974. Can. For. Serv., Marit. For. Res. Cent., File Rep. 19 pp.

In addition to examining growth loss from defoliation, our study was designed to look at the rate and amount of recovery of growth which could be expected if protection (insecticide spraying) were to follow several years of defoliation. This is particularly pertinent because the operational spraying strategy in areas such as New Brunswick has been to treat areas in imminent danger of mortality (Kettela 1975). Kleinschmidt et al. (1980) have shown that substantial growth losses can still occur during 1 to 2 years of protection following 3 to 4 years of severe defoliation; however, no data presently exist on the rate and amount of recovery with protection.

PLOT ESTABLISHMENT

Ten 0.025-ha plots were established in the Crowdis Mountain area of Cape Breton (Fig. 1) within 300 m of each other on similar forest sites. During 1976, budworm larvae consumed from 65 - 100% of the current year's foliage of trees on all the plots, but no backfeeding occurred on older age classes of foliage. In the spring of 1977, a spraying program was initiated to protect four of the plots (two spaced and two unspaced), to serve as controls for four additional defoliated plots (also spaced and unspaced). Each year from 1977 to 1981, the protected plots were sprayed before budworm feeding began, and they will be sprayed annually throughout the experimental period. A hydraulic sprayer with an 80-m hose was used to spray each tree in the protected plots with Dylox. Scaffolding was used in many instances to ensure adequate coverage of all the foliage. These operations have proven to be very successful in protecting foliage, and examinations each year have noted a maximum of 5% defoliation in any age class of needles. Figure 2 shows protected (P-1) and defoliated (D-1) plots, and a sample branch from each plot.

In addition to the eight protected and defoliated plots, two plots are being used to study the recovery of tree growth after several years of defoliation. The first recovery plot (R-1) was located in an area where all the tree foliage (current plus all older age classes) was consumed by an extremely high local budworm population in 1977. There was a maximum of 20% of the older-age-class foliage remaining on the lowest three or four branches on any tree in this plot. This probably represents the extreme of budworm feeding damage that is possible in one year. Plot R-1 has been sprayed from 1978 to the present. The second recovery plot (R-2) was first sprayed in the spring of 1980, prior to budworm feeding, and thus represents recovery after four years of defoliation. The recovery plots will continue to be protected until the trees regain their predefoliation growth rates. The type and number of the 10 plots used in this paper are presented in Table 1.

The plots were 0.025 ha, either square (15.8 x 15.8 m) or rectangular (12 x 20.9 m). However, we actually sampled a 0.05-ha area for each of the spaced plots (circular, 25.2 m diameter, using the same center as the 0.025-ha plot), in order to increase the sample size for stand data, and to allow direct comparison with data from mortality plots in the Cape Breton Highlands (see MacLean 1979). Only 0.025 ha was sampled for the unspaced plots because of the large number of trees present. Some of the data gathered in this study were from all trees in the plot, while other, more intensive defoliation and biomass measurements were made on a subset of trees in the plots.

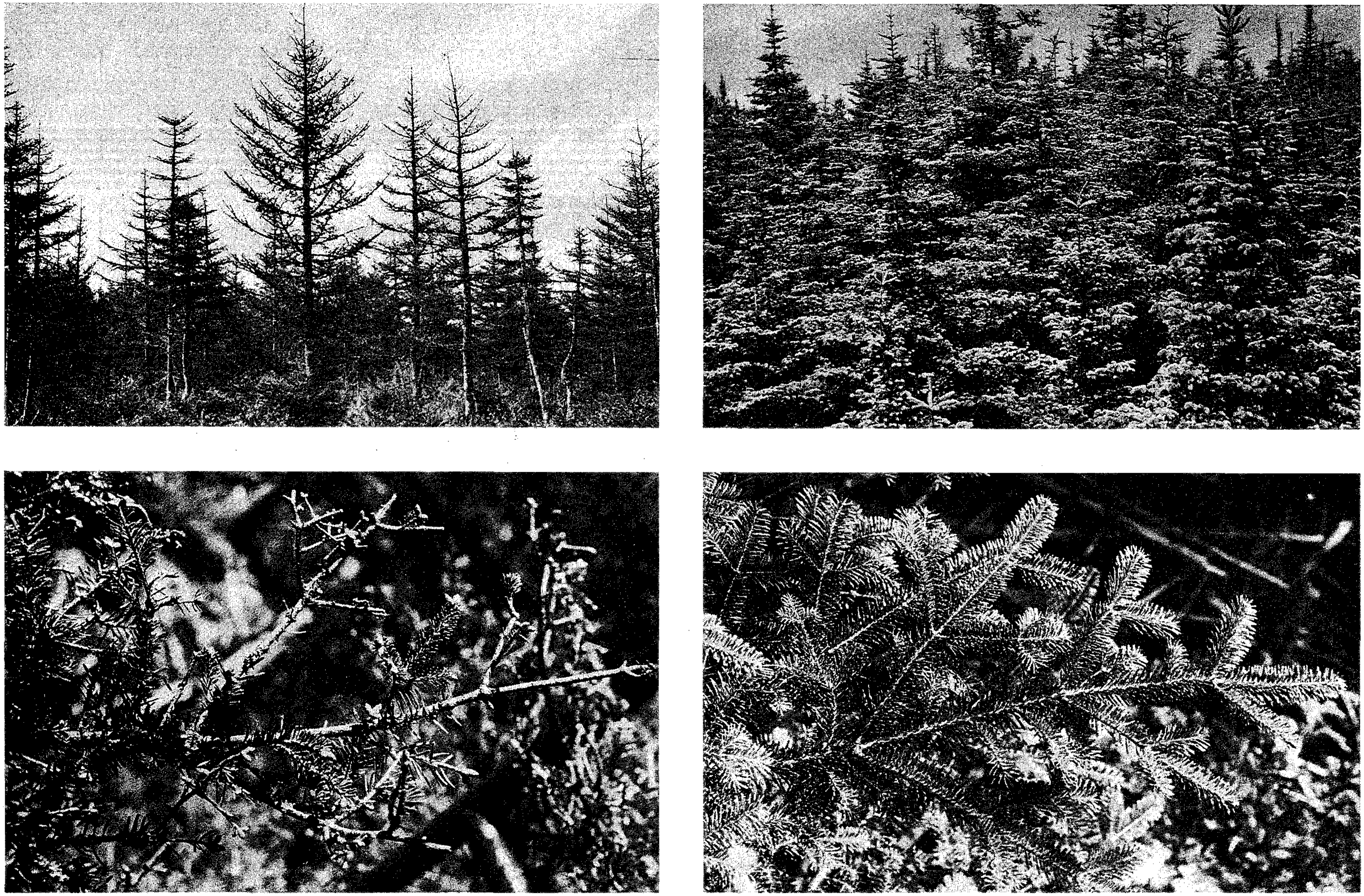

Fig. 2. Appearance in 1980 of the spaced protected and defoliated plots in a 25-year-old balsam fir stand on the Cape Breton Highlands and sample branches from each of the plots.

Table 1. Type and number of the ten 0.025-ha plots established in young balsam fir stands on the Cape Breton Highlands

Plot type	Treatment			
	Spaced		Unspaced	
Protected[1]	P-1	P-2	P-3	P-4
Defoliated	D-1	D-2	D-3	D-4
Recovery[2]	R-1	R-2		

[1] Sprayed with Dylox, annually from 1977 to the present, to protect the foliage from defoliation.

[2] Plots established to study the recovery of growth after several years of defoliation. R-1 was sprayed annually from 1977, and R-2 from 1980, to the present.

DATA COLLECTED FROM ALL TREES IN THE PLOTS

All trees in the plots were numbered and mapped by measuring the distance and compass bearing from the center of the plot. The following measurements were taken for each tree: dbh, height, height of bottom of crown (to allow calculation of crown length), crown widths (in north-south and east-west directions), and top condition, including length of bare top and height of the highest current year's growth.

All trees were checked annually for mortality, and beginning in 1980 all trees were rated for total defoliation (all age classes of foliage) and current defoliation. Total defoliation of each tree was rated visually by comparing the total crown of the sample tree with a fully-foliated crown. Defoliation rating consisted of 25% intervals, with one additional class for greater than 90% total defoliation (Table 2), and allowed for differentiation of trees with bare tops (greater than 60 cm, or 2 ft in length). This classification for total defoliation was originally developed by the Forest Insect and Disease Survey at Maritimes Forest Research Centre for Cape Breton mortality plots (Sterner et al. 1977, Magasi 1978), and was used in the present study. Good agreement has been found between trees in the >90% total defoliation class and tree mortality the following year (Magasi 1978, Ostaff 1979). Current defoliation of each tree was rated by scanning the crown with binoculars and estimating the average defoliation of current shoots on the tree using a scale (Table 3) modified from Fettes (1950). The midpoints of the defoliation classes for individual trees were used for calculation of plot averages (Tables 2 and 3).

Table 2. Classes used in visually rating total defoliation of individual trees

Class	Category	Midpoint[1]
1	Healthy and no defoliation	0
2	Healthy and only current defoliation	7.5
3	More than current but <25% total defoliation	12.5
4	26-50% total defoliation - no bare top	37.5
4a	26-50% total defoliation - with bare top	37.5
5	51-75% total defoliation - no bare top	62.5
5a	51-75% total defoliation - with bare top	62.5
6	76-90% total defoliation - no bare top	82.5
6a	76-90% total defoliation - with bare top	82.5
7	>90% total defoliation - no bare top	95
7a	>90% total defoliation - with bare top	95

[1] For calculation of plot averages.

Table 3. Classes used in visually rating current defoliation of individual trees

Class	Percentage defoliation of current shoots	Midpoint[1]
0	0-10	5
1	11-20	15
2	21-40	30
3	41-60	50
4	61-80	70
5	81-99	90
6	100	100

[1] For calculation of plot averages.

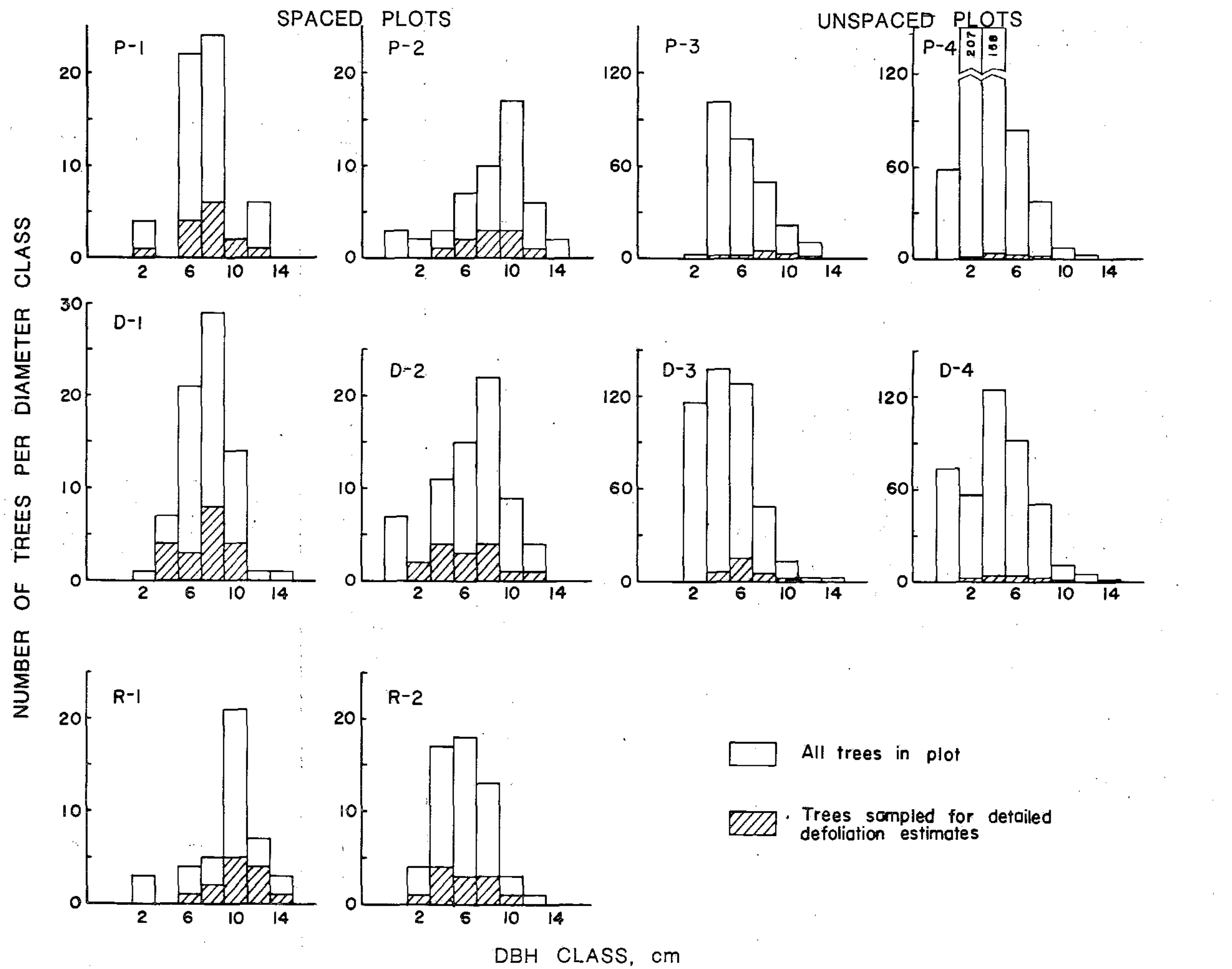

Fig. 3. Diameter distribution of all trees in 0.025 ha plots and trees sampled for detailed defoliation and needle biomass measurements in Cape Breton impact plots.

DATA COLLECTED FROM A SUBSET OF TREES IN THE PLOTS

Detailed Defoliation Estimates

In addition to the visual estimates of current and total defoliation on all plot trees, detailed annual assessments of feeding on each age class of needles were carried out for a subset of the trees in each plot. We selected sample trees which represented the range of diameters of trees within each plot (Fig.3).

Defoliation for a given year was estimated in the spring of the following year, prior to insect feeding (i.e., 1976-defoliation was estimated in the spring of 1977). Scaffolding was set up adjacent to each sample tree, and one branch was selected from each whorl, starting at the top and proceeding in a spiralling fashion down the tree to the 13th or 14th whorl on the spaced trees or the 10th or 11th whorl on the unspaced trees. Total length and width of the sample branches were measured, and the number of buds was recorded each year. Defoliation was also estimated on these same sample branches, each year. The second order branches within each sample branch were used as discrete sampling units (Fig.4). Within each secondary branch, all shoots of each age class of needles were individually rated for defoliation using the eight classes illustrated in Fig. 5; that is, all of the shoots in the current age class of needles, the one-year-old age class, and all other age classes present on the branch, were individually tallied by defoliation class each year. Although the illustration of defoliation classes in Fig. 5 is an obvious oversimplification (balsam fir shoots are not two-dimensional), it was found useful in training observers.

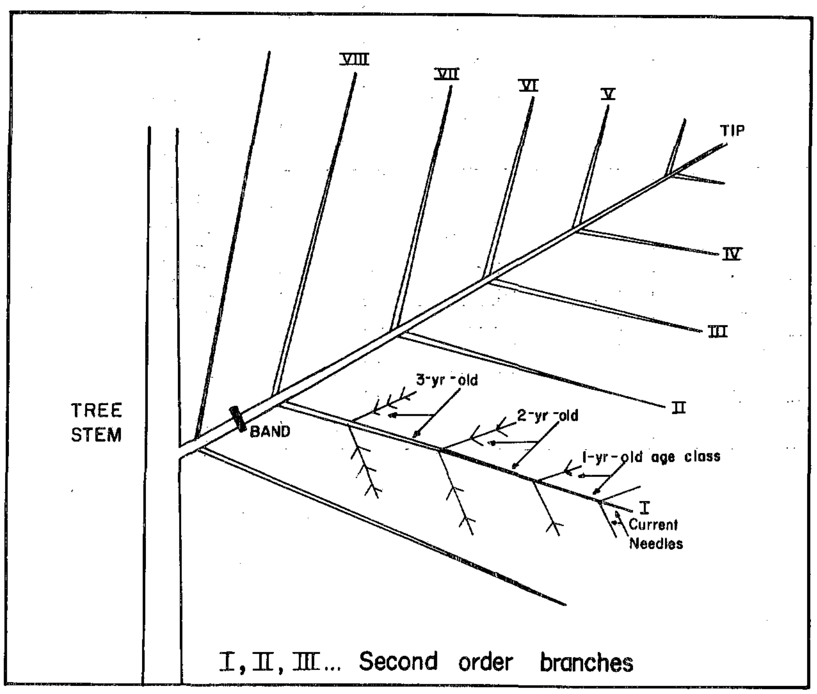

Fig. 4. Arrangement of second order branches and age classes of needles on a balsam fir sample branch. The second order branches were used as discrete sampling units within each branch.

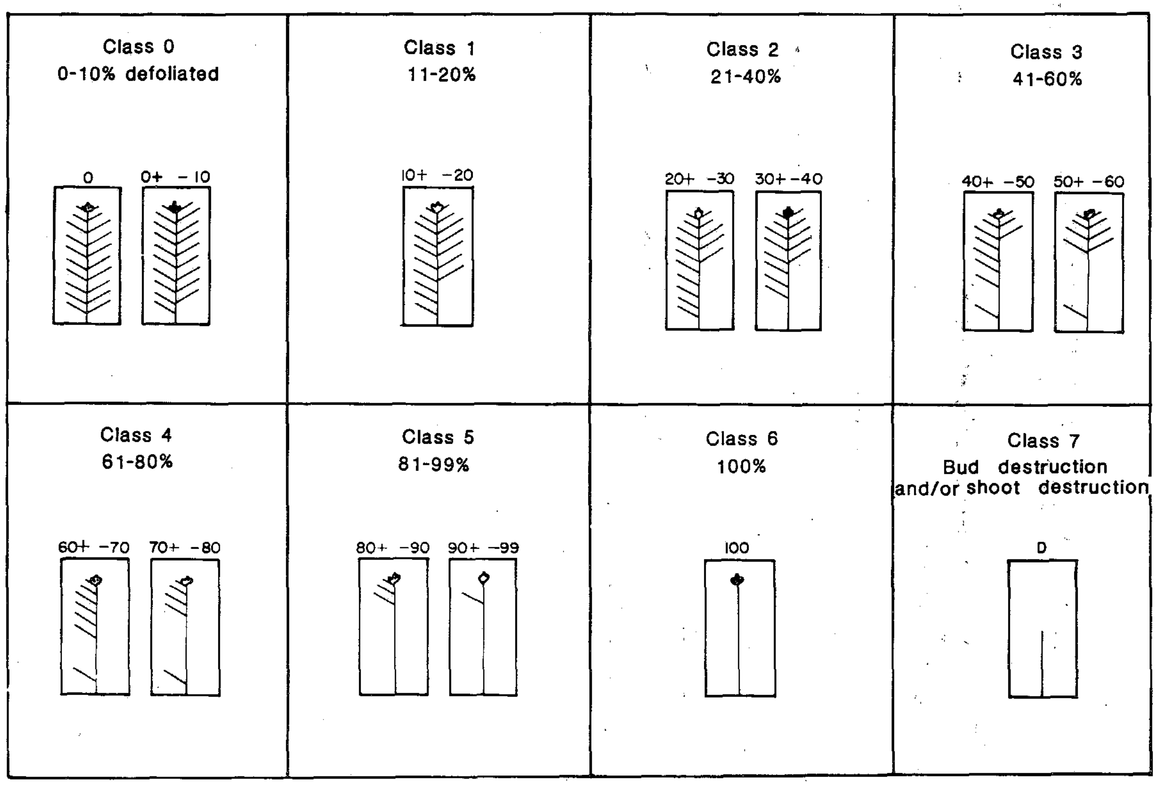

Fig. 5. Illustration of classes used in determining detailed defoliation estimates (modified from Fettes 1950).

The accuracy and precision of visual defoliation estimates on individual balsam fir shoots were tested by MacLean and Morgan (1981). Visual estimates of defoliation on over 500 shoots from 25-year-old fir trees were compared with actual defoliation values calculated from the number of needles remaining on the shoot after defoliation and the original number of needles, which was determined from the phyllotaxis (spiral arrangement) of leaf scars on the shoot (see MacLean and Morgan (1981) for methods). An inverse relationship was found between the amount of defoliation on a shoot and the visual estimation error. Estimation error increased from 0.9% for shoots that were 81-99% defoliated, to 4.3% for shoots in the 61-80% defoliation class, to 9.2% for the 41-60% class, to 10.8% for the 21-40% class, to the maximum of 16.0% for the 0-20% class. For shoots that were 81-99% defoliated, the visual method overestimated defoliation slightly, while errors on shoots with less than 80% defoliation were usually underestimations. These visual estimations of defoliation were based on results of only one observer, and indicated that the most serious source of error in the estimates was introduced when the observer tended to overlook missing needles on shoots which approached the fully foliated condition. However, for shoots with >20% defoliation, error was generally less than 10%, which is an acceptable level. In practice, several observers of defoliation were used in the field; they were trained and their estimates were checked until we were satisfied with their accuracy.

From 1977 to 1979, defoliation was estimated on one branch per whorl on each of the sample trees, or an average of 12 and 10 branches for spaced and unspaced trees, respectively. Data for 13 trees from plot D-1 and 8 trees from D-3 were analyzed to determine the within-tree sampling intensity required for a given level of precision. Budworm populations in 1977 and 1978 were extremely high, with averages of 70 and 75, 6th-instar larvae per 45-cm branch tip. In both years, the current foliage was consumed in the bud stage and severe backfeeding of older age classes of foliage occurred. In 1979, budworm populations decreased to about 25 larvae per 45-cm tip, only part of the current foliage was consumed and no backfeeding occurred. In determining the number of branches required for defoliation estimation, we considered data on the 2-, 3- and 4-year-old age classes of needles for 1977 and the 3- and 4-year-old age classes for 1978. Older age classes were omitted because of natural needle fall. In 1979, only the current age class of needles was considered. For each tree, we calculated average percentage defoliation based on (a) all the branches sampled on the tree, (b) every second branch, (c) every third branch, and (d) every fourth branch; the means were then compared (Table 4). A deviation of ± 5% from the mean defoliation was considered acceptable, based on the accuracy of visual estimates of defoliation (MacLean and Morgan 1981). Table 4 shows that for both 1977 and 1978 defoliation estimation based on measurements for every second branch was acceptable, while estimations for every third and fourth branch increased the deviation above the acceptable level. In 1979, defoliation estimates of current foliage on every third branch were acceptable (Table 4). Based on this analysis, we decreased the sampling intensity from 1980 onward by sampling every second branch. In analyzing the data for 1977 and 1978 (age class 2 to 4) we consistently observed that levels of defoliation decreased from the top to

Table 4. Deviation from the mean defoliation caused by including only branches from every second, third, and fourth whorl for different age classes of foliage from defoliated trees

Year	Plot	Age class	Mean defoliation %	Deviation from the mean					
				Every-2nd[1] whorl	S.E.[2]	Every-3rd whorl	S.E.	Every-4th whorl	S.E.
1977	D-1	2	74.4	3.1	0.6	5.0	0.9	5.2	0.9
	"	3	54.2	4.3	0.7	5.7	0.8	8.7	1.7
	"	4	41.4	4.4	0.7	7.7	1.1	9.2	1.7
	D-3	2	63.5	5.3	0.8	8.0	1.1	10.8	2.3
	"	3	40.5	5.7	1.0	7.7	1.4	11.1	2.7
	"	4	22.2	5.6	1.4	6.1	2.3	8.0	2.9
1978	D-1	3	17.5	2.9	0.7	4.3	0.9	4.9	0.9
	"	4	32.3	3.3	0.8	6.5	1.0	7.1	1.2
	D-3	3	16.9	3.0	0.6	7.2	1.4	6.4	1.9
	"	4	28.1	4.2	0.8	9.4	1.9	9.2	1.2
1979	D-1	current	75.1	2.8	0.4	4.4	0.7	7.0	1.2
	D-3	"	80.5	4.2	0.7	4.9	1.0	7.1	1.4

[1] Measuring every second, third, or fourth branch.

[2] S.E. = Standard error.

the base of the trees, but this relationship was not evident for the current foliage in 1979.

Determination of Foliage Biomass

In 1976, 1977, and 1978, current defoliation in the unprotected plots was nearly 100%, but in 1979, the budworm population dropped drastically, and current defoliation ranged from 70 to 90%. As a result of prolific shoot production by the defoliated trees in 1979, foliage remaining on the trees could not be accurately estimated from comparisons with the protected trees, and a method for non-destructive estimation of the foliage by age class on standing fir trees was required.

A method for estimating foliage biomass was found from the analysis of interrelationships between weight, needle length, and shoot length of fir shoots (Piene 1981)[2]. Needle weight was found to be a function of mean needle length, while the number of needles per centimetre of shoot was found to be related to the reciprocal of needle length (Piene 1981)[2]. These two relationships were combined, such that weight of needles per shoot could be predicted from data on mean needle length and mean shoot length for the branch (Fig. 6).

[2] Unpublished.

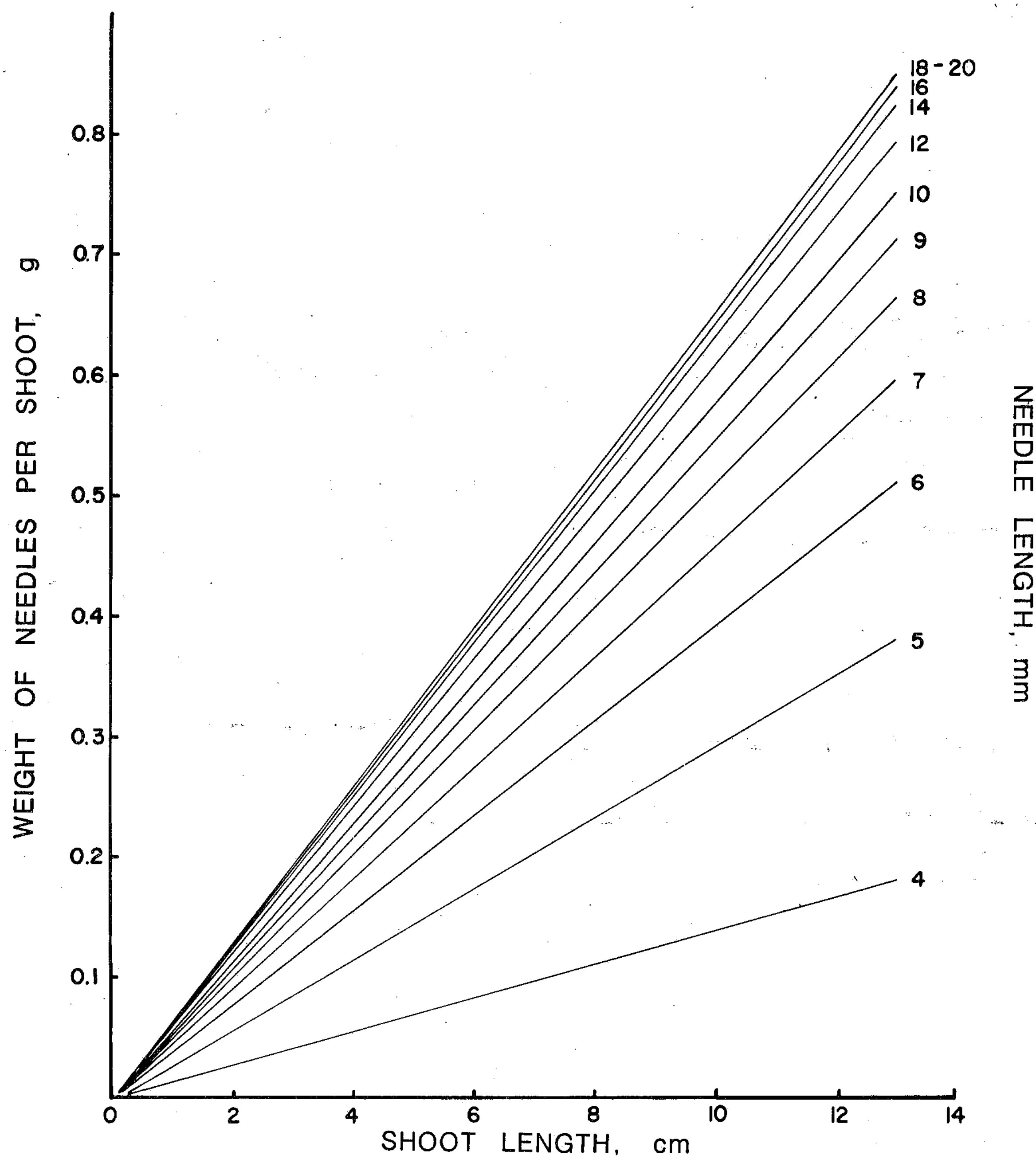

Fig. 6. Relationship for predicting weight of needles per shoot as a function of mean needle length and shoot length (Piene, unpublished).

Actual methodology for determining foliage biomass was as follows. For each age class of needles, 10 shoots were selected from the entire branch, and the length of five needles from the middle one-third of each of 10 shoots was measured to the nearest millimetre. Mean needle length for each age class was calculated from the 50 sampled needles. The lengths of all shoots in every age class were measured on each second order branch, and then the number of shoots remaining on the rest of the branch was counted. Mean shoot length was then calculated:

Mean weight of needles per shoot = f(mean shoot length, mean needle length) (Fig. 6) (1)

Potential total weight of needles per branch = Σ no. shoots x mean wt. needles per shoot (2)

Actual total weight of needles per branch (after defoliation) = Potential needle wt. (Eqn. 2) x percent defoliation (3)

These measurements and calculations determined the weight of each age class of needles per branch.

In addition to this non-destructive determination of foliage biomass on the sample trees within the plots, 24 trees from outside the plots were destructively sampled between 1977 and 1979. Diameter at breast height, height, height of each whorl, total lengths and widths of each branch and its foliated portion, and branch diameter were recorded for each tree. Branches were then dissected by age class of foliage; age classes of foliage were separated into needle and twig components, and these were oven-dried (100°C for 24 h) and weighed. Analysis of data from the destructively sampled trees allows the calculation of allometric relationships between foliage weight and branch dimensions, and generally allows a more detailed analysis of foliage biomass of the defoliated and protected trees.

Determination of Volume Growth

Because trees record their growth in the annual rings, most analyses of volume growth of the defoliated and protected trees will be conducted at the end of the experimental period. This will involve felling the trees, measuring inter-whorl distances, cutting discs from the stem of the tree, and measuring the width of the annual rings in the discs using a Holman Digimicrometer[3] ring measuring machine. Data on ring widths and distances between sampled discs allow calculation of the current annual volume increment of the tree, which is a more satisfactory assessment of growth than is radial increment or total volume.

A total of 24 trees, with discs taken from every internode, was analyzed to determine the number of discs required from the tree stem to calculate volume growth accurately. Current annual volume increment was calculated for each of the last 10 years of growth, based on the complete disc series, and also on a partial series including discs from only every 2nd, every 3rd, and every 4th whorl. The partial series started at the top of the tree, and, in all cases, included the top and bottom discs taken from the tree. For the approximately 30-year-old fir trees in this study, taking a disc from every 2nd whorl resulted in a total of 11 to 15 discs per tree, from every 3rd whorl in 8 to 10 discs, and from every 4th

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3 Manufactured by Holman Electronic Controls Ltd., Fredericton, N.B., Canada. Distributed by Hayward Business Products Ltd., P.O. Box 692, Fredericton, N.B., Canada.

in 6 to 8 discs per tree. Mean deviations from the current annual volume increment calculated from the complete disc series averaged 3.6% for discs from every 2nd whorl, 5.4% from every 3rd, and 7.7% from every 4th whorl (Table 5). The deviations were almost equally divided between overestimates and underestimates; there was no consistent bias. The maximum deviation for individual trees increased considerably by taking a disc from every 3rd whorl to every 4th whorl: three trees had deviations greater than 20% with every 4th disc sampling. Therefore, it was decided to use the sampling intensity of discs from every 3rd whorl in future analyses of volume growth in this study. Other less detailed studies could possibly use fewer discs per tree, and still have a fairly accurate estimate of current annual volume increment.

Estimation of Insect Populations

Budworm population density was not recorded in 1976. Beginning in 1977, a 45-cm branch tip was collected yearly from one midcrown branch from each of ten trees located outside the boundary of each of the P-1, P-3, D-1 and D-3 plots, and the number of 6th-instar larvae and buds were recorded. In addition, in 1978 yearly counts of egg masses and 2nd-instar larvae were begun for a plot about 200 m from the P-1 plot.

NUTRITIONAL AND PHYSIOLOGICAL CHANGES IN FOLIAGE FROM DEFOLIATED TREES

Changes in average needle length, number of needles per centimetre of shoot length, and needle weights were measured annually on current foliage collected from 10 trees located around the boundary of the two recovery plots. About 70 shoots were sampled per tree. The shoots (terminals and sub-terminals) were collected from the outer one-third of south-facing branches from whorls 4 to 10. Average needle length for the middle one-third of the shoot, and associated dry weights of needles for each shoot (dried at 60°C for 48 h) were determined. Also, changes in percent N, P, K, Ca, and Mg were determined annually from a subsample of the shoots from each tree, using methods outlined in MacDonald (1977).

Morphological changes in needles from defoliated trees near the recovery plots are being studied by K. Percy, Maritimes Forest Research Centre. In October 1980, current, 1-, and 2-year-old foliage samples were collected from the R-1 and P-1 plots, and current foliage was collected from the R-2 plot. Two trees were selected outside each plot, and nine needles were collected from the middle one-third of the terminal shoot of two adjacent south-facing branches on whorl 5.

Five millimetre sections were excised from the mid-section of each needle. The sections were fixed in formalin acetic-acid-alcohol (FAA), and dehydrated through a tertiary-butyl alcohol series, embedded in paraplast, sectioned at 10μ on a rotary microtome, and mounted on chemically cleared slides (Johansen 1940). The needle sections were stained with safranin fast green (Johansen 1940) and examined for general morphological detail.

Attempts are also being made to relate physiological stress caused by defoliation to readings from a Shigometer[4] which measures electrical resistance in the cambium. Measurements have been made on several trees from each of the plots. This study was initiated in 1979 and is under the direction of Dr. D.S. Fensom, Mount Allison University, Sackville, N.B.

4 Shigometer, Model 7950. Manufactured by Northeast Electronics Corp., Concord, New Hampshire, U.S.A.

Table 5. Mean deviation (%) from the current annual volume increment calculated from the complete disc series) of balsam fir trees caused by including discs from only every second, third or fourth whorl. Deviation presented is the mean for the last 10 years growth for each tree

Tree No.	Plot[1]	Deviation from the current annual volume increment (%)					
		Every-2nd disc		Every-3rd disc		Every-4th disc	
		$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.
1	P-2	2.0	0.5	5.4	1.5	24.0	7.7
2	D-2	2.9	0.9	4.7	1.4	5.6	1.1
3	P-2	3.9	1.1	3.0	0.5	3.4	0.4
4	D-2	2.6	0.5	3.4	0.8	2.0	0.5
5	P-2	5.5	1.9	16.7	7.1	28.6	12.5
6	D-2	0.7	0.3	2.5	0.5	4.2	0.8
7	P-1	3.3	0.7	5.3	1.0	7.6	1.2
8	D-1	6.4	1.9	14.0	3.0	12.6	4.9
9	P-1	5.5	1.0	2.1	0.4	3.2	1.5
10	D-1	2.4	0.7	3.1	0.6	6.3	1.1
11	D-1	2.3	0.5	6.8	1.3	3.0	0.7
12	D-1	3.6	0.4	5.8	0.9	5.3	0.8
13	D-1	2.8	0.8	3.7	1.2	7.5	1.2
14	P-1	1.0	0.2	2.6	0.5	2.2	0.5
15	D-1	7.6	2.6	9.8	2.1	20.4	6.8
16	D-1	3.4	1.5	3.6	0.8	6.2	1.3
17	D-1	3.3	0.7	8.1	1.2	8.9	2.3
18	D-1	5.0	0.9	3.5	1.5	5.3	1.2
19	D-1	4.4	0.7	5.7	1.3	7.5	2.0
20	D-3	2.6	0.8	4.9	1.1	4.3	0.9
21	D-3	4.9	1.0	3.6	1.0	5.1	1.2
22	D-3	0.8	0.2	1.7	0.7	2.7	0.5
23	P-3	3.3	0.6	2.0	0.4	3.8	0.9
24	P-3	5.4	0.5	6.6	0.6	4.0	1.1
Mean for all trees		3.6	0.4	5.4	0.8	7.7	1.4

[1] Trees were sampled outside the periphery of each plot.

ATTACK BY SECONDARY INSECTS AND DISEASES

Since 1978, trees from the defoliated plots were examined annually for decays and associated insect activity in the main stem. In 1978 and 1979, several of the most heavily defoliated trees were destructively sampled and examined for expected stem defects as described by Basham (1959) and Stillwell and Kelly (1964). In 1980, 10 trees each from the boundaries of plots D-1 and D-3, and from a nearby mature stand were randomly selected and examined. Ten trees from outside each plot will be examined annually. Sample trees were felled in late September or early October, the amount of sap rot and associated insect activity, and heart rot (trunk rot and butt rot) and probable causes were recorded to determine if budworm activity contributed significantly to the normally low level of these defects on the Cape Breton Highlands (Davidson 1957). The bark was removed from the stem of the sample trees, and the underlying sapwood was examined for discolorations and evidence of insect activity. The stems were sectioned into 1-m lengths and the cross-sectional area of the stem and any decays or discolorations were plotted on height-area graphs. Total stem volumes and decay volumes were calculated from the areas under each curve.

Tree sections with decay or extensive stain were split longitudinally in a transfer chamber and small chips were aseptically removed from the margin of the defective area and placed on malt extract agar. Fungi growing from these chips were identified. The fungi that were cultured plus evidence of particular insect activity were recorded on the height-area graphs adjacent to the particular defect.

Defoliation estimates were made from two opposite branches from the midcrown of each sample tree. Mean needle length and shoot length of each age class of foliage were measured as described in an earlier section, and the dry weight of needles remaining on the shoots was determined. Expected foliage weights were determined from needle and shoot lengths based on the relationships in Fig. 6, and the percent defoliation for each age class was calculated as:

$$(\text{Expected foliage weight} - \text{actual foliage weight}) \div \text{expected foliage weight} \times 100. \quad (4)$$

The percent defoliation for each year not obviously affected by normal needle fall was plotted on a graph, and the area under each curve divided by the total area of the graph was used to derive an overall percent defoliation. This value gave a rough index of the budworm damage that the tree had sustained since 1976, which could be compared to the relative amounts of the various types of decay.

CONTINUATION OF THE STUDY

Spruce budworm population level in the study area was still high in 1980, and the forecast, based on egg mass and 2nd-instar larval counts for 1981, gives no indication of reduced levels. We plan to continue the study of growth loss until the population of spruce budworm subsides, and to follow the recovery growth plots until the trees have regained predefoliation growth rates.

The main objectives of the present study on both an individual tree and stand basis include:

(1) To relate a known decrease in foliar biomass on spaced and unspaced balsam fir trees, caused by defoliation, to a reduction in volume growth for each year and/or a sequence of years in the study period.

(2) To relate the loss in foliar biomass over time to the onset of secondary insect attack and decay.

(3) To relate the defoliation

history or the loss in foliar biomass to the subsequent production of new foliage.

(4) To determine the time required for balsam fir trees with different defoliation histories to recover to predefoliation growth rates (stem and foliar biomass) when foliage protection (spraying) is applied.

(5) To determine if a relationship exists between stem growth rate and foliar biomass production in stressed trees.

(6) To define intra- and inter-tree variance in stem and foliar biomass growth and define a sampling technique to measure these variables.

(7) Assuming that a measure of the foliar biomass remaining on the tree after attack is the best prediction of the fate of the tree, to determine if the detailed methods of this study can be compressed into a broad-scale survey tool.

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