IMPACT OF DEFOLIATION BY SPRUCE BUDWORM POPULATIONS ON RADIAL AND VOLUME GROWTH OF BALSAM FIR: A REVIEW OF PRESENT KNOWLEDGE

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ABSTRACT

Epidemic populations of the spruce budworm (Choristoneura fumiferana Clem.) have resulted in severe defoliation of host tree species over much of eastern North America. This paper reviews the effects of defoliation on radial and volume growth of balsam fir (Abies balsamea (L.) Mill.) trees and stands. Several studies since the 1920's have shown that growth increment is reduced about 50 to 75% by several years of severe defoliation. Recent studies of defoliation impact on balsam fir in eastern Canada and the United States have found that:

1) Reductions in volume increment of young fir trees were evident during the first year of defoliation, and severe defoliation for 2 years resulted in a 50% reduction in volume growth.

2) Expressed on a stand basis, stands which suffered light defoliation (< 20% of current foliage) for 5 years showed negligible growth loss, whereas severe defoliation (> 90% of current foliage) for 5 years resulted in a 60% annual growth loss.

3) Defoliation during a budworm outbreak in the 1950's resulted in greatly reduced diameter growth and virtually no height growth. After the collapse of the outbreak, diameter and height growth of surviving trees were similar or greater than that in unaffected stands. However, recovery on a stand basis was poor; only one plot out of 10 had regained its predefoliation volume 15 years after defoliation ceased.

Key words: Abies balsamea, defoliation, growth loss, spruce budworm.

INTRODUCTION

The spruce budworm (Choristoneura fumiferana Clem.) is a forest insect which is economically very important in eastern Canada and the United States. Periodically, this insect erupts from its generally low population levels and causes widespread defoliation of host trees over large areas. It passes through six larval life stages before pupating into a moth; it is during the last larval stage (sixth instar) that it does most (87%) of its feeding and causes most defoliation (Miller 1977). Budworm populations generally build up gradually over several years, with the increased defoliation becoming noticable upon casual viewing. This removal of a portion of the tree's needles, the photosynthesis factory, results in decreased growth or wood production, first at the top of the tree where defoliation is most concentrated initially. Persistent severe defoliation will kill trees after three to six years (MacLean 1980), and dead stands over extensive areas may result. A generalized scheme of the timing of events during a hypothetical budworm outbreak is presented in Figure 1.

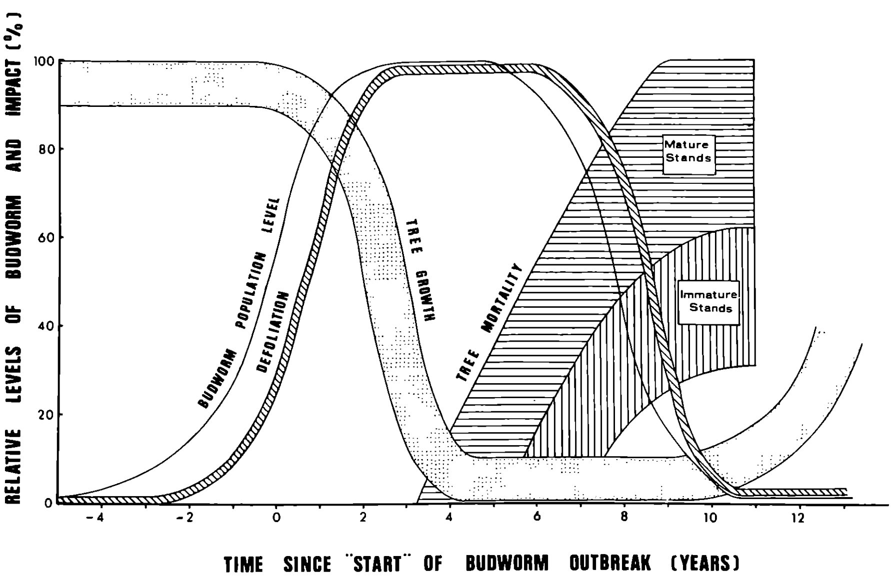

Figure 1. Relative levels of spruce budworm populations and impact in relation to time during a hypothetical outbreak.

The subject of this paper is the impact of defoliation on growth loss, both in terms of reduction of radial growth (or annual ring widths) of individual trees and reduction of volume growth of both trees and stands. It has been known for many years that defoliation results in reduced radial increment, but few data are available to quantify a functional relationship between varying degrees of defoliation and reduction of radial and volume growth. In this paper, I review the effects of defoliation on growth of the major host tree species, balsam fir (Abies balsamea (L.) Mill.), and discuss the results of three recent studies which have helped to better quantify impact. The limited data available on growth loss of the other host tree species, including white spruce (Picea glauca (Moench) Voss), black spruce (Picea mariana (Mill.) B.S.P.) and red spruce (Picea rubens Sarg.), are also discussed.

REDUCTION OF RADIAL INCREMENT IN INDIVIDUAL TREES

Details of the methods and results of eight studies of the loss of radial increment resulting from defoliation by spruce budworm are summarized in Table 1A. Most of these studies have examined only balsam fir, and have found growth loss ranging from 30 to 75% of the predefoliation annual increment. Several of the earlier studies were mainly concerned with showing that defoliation caused a growth loss, and did not quantify the loss of radial increment.

Methods of determining growth loss in these studies have ranged from examination of increment cores or discs taken at breast height or stump height, to examination of a few discs taken from different heights on various trees, to complete stem analysis of discs from every internode of the sample trees. Duff and Nolan (1953) showed by complete stem analysis that there are species-specific patterns of radial growth of trees in relation to height, and demonstrated this in terms of three ring sequences of red pine (Pinus resinosa Ait.), which they called Type 1, 2, and 3 sequences. Mott, Nairn, and Cook (1957) found that the patterns in ring widths of balsam fir are similar to those found by Duff and Nolan (1953), and noted that the effects of defoliation on growth were evident in all three sequences. However, Type 1 (oblique) and Type 3 (vertical) ring sequences best showed the effects of defoliation on radial increment. Both Mott et al. (1957) and Williams (1967) have shown that the greatest reduction in radial increment resulting from defoliation is in the mid-crown, and the least is near the ground. Thus, the results of most of those studies (Table 1A) that were based only on radial increment in the lower bole do not reflect average tree conditions, and are of limited use in predicting loss of wood production on a stand basis. In addition, growth loss is ultimately a function of the severity of feeding in individual years and of the number of years of

Table 1. Summary of studies of loss of radial and volume increment of trees resulting from defoliation by spruce budworm populations

Reference	Methods	Tree species	Growth loss (%)	Time lag (yrs)[1]
A. Radial Increment Loss Data				
Craighead 1924	Sampled 3 discs per tree from 12-14 trees of each species. Growth loss calculated in relation to ring width of the first year preceding feeding.	*Abies balsamea* (L.) Mill. *Picea rubens* Sarg. *Picea rubens*	60-70[2,3] 50-60[2,3] 50-90[2,4]	0-1
Belyea 1952	Dendrometer measurements at breast height on 94 trees, for 6 years.	*Abies balsamea*	not quantified[5]	2
McLintock 1955	Increment cores at breast height from about 100 trees. Growth loss calculated by comparison with growth in the 5-year period preceding defoliation.	*Abies balsamea*	60-75	2-5
Mott, Nairn and Cook 1957	Complete stem analysis of 2 trees and partial stem analysis of 10 trees.	*Abies balsamea*	not quantified[5]	1-2
Blais 1958	Increment cores from 50 trees in each of 6 plots.	*Abies balsamea*	not quantified[5]	2-4

Table 1. Cont'd

Reference	Methods	Tree species	Growth loss (%)	Time lag (yrs)[1]
Blais 1964	Discs at stump height from 50 fir, 33 white spruce and 4 black spruce trees. Growth loss calculated by comparison with growth in the 10-year period preceding defoliation.	Abies balsamea Picea glauca (Moench) Voss Picea mariana (Mill.) B.S.P.	46 36 18	-
Williams 1967	Partial stem analysis (6 discs per tree) of 10 trees in each of 4 damage classes. Growth loss calculated by comparison with growth in the 10-year period preceding defoliation.	Abies grandis Dougl. (Lindl.) Picea engelmanii Parry	24-41 4-25	- -
Miller 1977	Discs at stump height.	Abies balsamea	27-53	-
B. Volume Increment Loss Data				
Batzer 1973	Stem analysis of 3 trees from each of 8 plots. Paired plot design with one plot of each pair protected from defoliation by spraying insecticide.	Abies balsamea	25 (second yr) 80 (sixth yr)	1
Baskerville and MacLean 1979	Complete stem analysis of a defoliated tree and an undamaged tree. Growth and mortality losses of 10 plots were quantified on a per-plot basis.	Abies balsamea	25 (second yr) 36 (sixth yr) 75 (tenth yr)	-

Table 1. Cont'd

Reference	Methods	Tree species	Growth loss (%)	Time lag (yrs)[1]
Piene (in press)	Complete stem analysis of 25 trees that had suffered differential defoliation over 2 yrs. Growth loss calculated by comparison with a linear projection of previous growth.	Abies balsamea	20 (first yr) 50 (second yr)	0

1 Time lag between defoliation and growth loss based on the original estimate of time of initiation of the budworm outbreak.
2 Range of values represents mean growth losses after 2-5 and 6-9 years of feeding, respectively.
3 Growth loss of trees that survived the outbreak.
4 Growth loss of trees that died during the outbreak.
5 Graphically-presented growth data demonstrated a defoliation-caused growth loss, but the decrease was not quantified in the paper.

feeding, or the sequence of severity of defoliation in successive years. However, most of these studies have not differentiated among differing degrees of feeding or temporal sequences of defoliation.

Only limited data exist on growth loss of host tree species other than balsam fir. Reduction of radial increment of red spruce was found to range from 50 to 60% of the predefoliation increment for trees that survived the outbreak (Craighead 1924). Growth losses of white and black spruce were 36 and 18%, respectively (Blais 1964). Thus, the few data available support the conventional idea that damage is less in spruce, particularly black spruce, than in balsam fir.

A few points of interest have emerged from the studies of radial increment loss. Both McLintock (1955) and Miller (1977) noted that the loss in radial increment caused by defoliation was less in slow-growing than in fast-growing trees. Craighead (1924) found that growth loss of red spruce that survived a budworm outbreak was less than that of trees which died during the outbreak. Similarly, tree vigor (as expressed by increment at breast height) at the time of defoliation has been found to be related to incidence of tree mortality, with more rapid growth rates accompanying lower mortality (Craighead 1925, Morris 1946). However, under severe defoliation this relationship broke down, presumably because persistent severe defoliation can kill even vigorous trees. The feasibility of identifying past budworm outbreaks as series of years of suppressed growth in radial increment data has been demonstrated and discussed in detail by Blais (1962). The time lag between the initial defoliation and the first growth loss observed as reduced radial increment has been found to range from 0 to 5 years, with most of the early studies citing 2 to 5 years (Table 1A). However, results based on discs from the lower bole are useless in this regard, since the earliest and most substantial effects of defoliation on growth are in the upper or mid-crown. More recent studies have shown that effects on tree growth are evident during either the first or second year of defoliation (Batzer 1973, Piene in press).

REDUCTION OF VOLUME INCREMENT IN INDIVIDUAL TREES

Considering growth loss in terms of volume of wood production by individual trees overcomes certain limitations of the studies of radial increment loss. Volume increment calculations take into account the natural variability of the internal growth pattern (i.e., the differences in diameter growth at different heights on the stem). Also, volume increment includes effects of defoliation on height growth as well as radial growth, and budworm-caused defoliation is known to drastically affect height growth of balsam fir (Figure 2), and to result in top-killing of many trees in a stand. Three studies exist on loss of volume increment of balsam fir trees from defoliation (Table 1B); these are discussed in more detail.

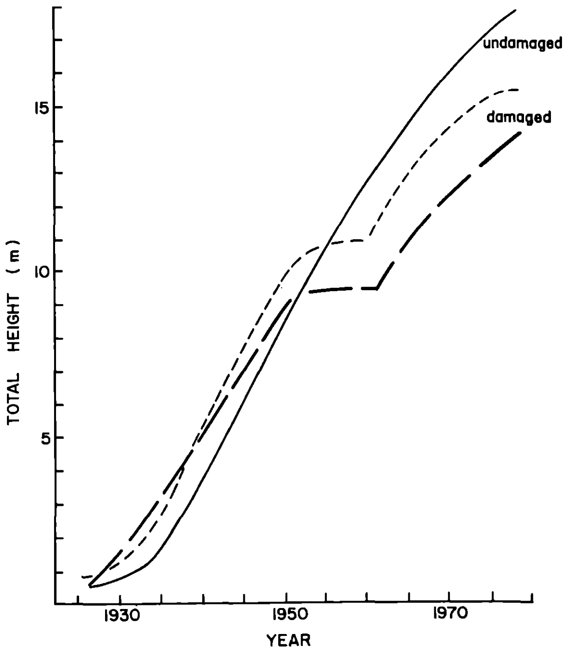

Figure 2. Development of height over time for two trees from a stand damaged by budworm and one tree from an undamaged stand. The effect of defoliation from 1950 to 1958 is shown (from Baskerville and MacLean 1979).

For seven years during an outbreak and five years after, Batzer (1973) studied defoliated spruce-fir stands and similar stands protected from budworm attack by insecticides in Minnesota, U.S.A. He presented graphically the considerable loss of volume growth of individual trees resulting from defoliation, but the loss was not numerically quantified. Estimates calculated (fig 2. Batzer 1973 p. 37) indicate that volume growth of defoliated trees was about 25% less than in protected (sprayed) trees in the second year of defoliation, and the loss increased to about 80% after the sixth year of defoliation.

Baskerville and MacLean (1979) have considered budworm-caused mortality and growth loss of balsam fir plots in northwestern New Brunswick, Canada, which were severely defoliated in the mid-1950's, and also the 20-year post-outbreak recovery of these plots, on a stand basis. Diameter increment of the trees decreased under defoliation, and height increment stopped; the combination of these two effects resulted in drastically decreased volume increment in the defoliated trees. Comparing a defoliated tree with a tree unaffected by defoliation (Figure 3), the current volume increment was about 25% less after 2 years of defoliation, 36% less after 6 years, and 75% less after 10 years.

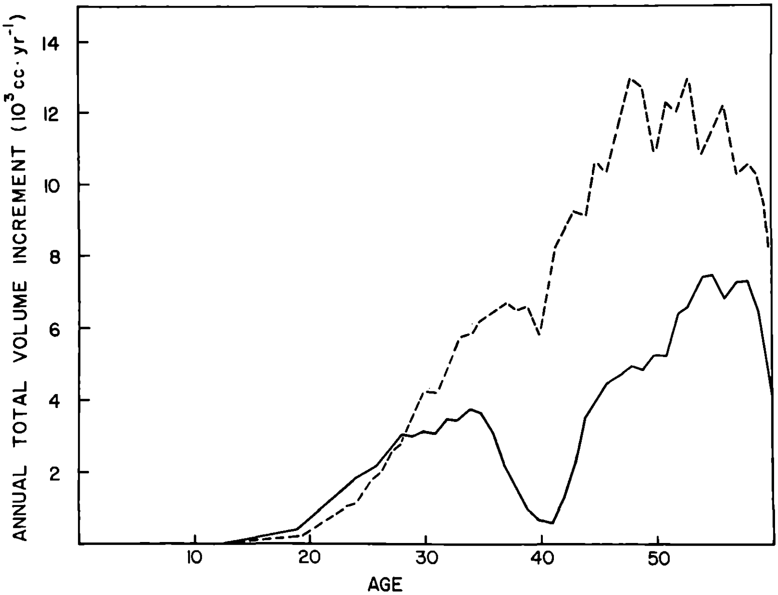

Figure 3. Annual volume growth of a tree unaffected by defoliation (broken line) and a tree suffering severe defoliation from age 28 to 40 years (solid line). (from Baskerville and MacLean 1979).

Although the results of Batzer (1973) and Baskerville and MacLean (1979) have helped to quantify the loss of volume increment of individual trees after several years of severe defoliation, neither of these studies recorded detailed estimates of defoliation on individual trees and linked defoliation directly to growth loss. However, a recent paper by Piene (in press) describes the results of such a study on 25-year-old balsam fir trees in Nova Scotia, Canada which received varying amounts of defoliation over a 2-year period. Defoliation was visually estimated on one branch per whorl for seven whorls in the upper and mid-crown, and growth was measured by stem analysis of discs from every internode. Defoliation during the first year ranged from 60 to 100% of the current year's foliage, and during the second year from 20 to 100%. Growth loss from defoliation was calculated by projecting the predefoliation volume increment as a "potential" growth had there been no defoliation; this was possible because the trees had undergone a spacing treatment (to 2.4 x 2.4 m) five years prior to the first budworm feeding, and had exhibited a linear increase in volume increment over the 5-year predefoliation period. Piene (in press) observed a loss in volume increment in the first year of defoliation, averaging about 20% of the volume increment for trees that had lost 80 to 100% of current foliage. Trees that lost a total of two age classes of needles (two years of accumulated defoliation) had volume growth decreased by about 50%. Piene also observed, as did several earlier studies, that the decrease in radial increment caused by defoliation was greater at mid-crown than at breast height.

LOSS OF VOLUME INCREMENT IN STANDS

Practical management of a forest resource requires information about the impact of defoliation on wood production on a stand basis. To understand how defoliation affects volume on a per hectare basis, it is first necessary to determine how individual trees react to defoliation; then results should be calculated as volume loss per hectare. Only two recent studies are currently available to provide data on this aspect. Kleinschmidt et al. (in press) have recently completed a study of 20 fir-spruce plots in Maine, U.S.A. with different defoliation histories. A 5-year defoliation history was estimated for each plot by comparing weights of foliage in each age-class of needles with the amounts produced by non-defoliated balsam fir trees; tree growth was assessed by stem analysis. Results of the study are summarized in Table 2, and show that stands which suffered light defoliation (< 20% of current foliage) for 5 years showed negligible growth loss, whereas severe defoliation (90 to 100% of current foliage) for 5 years resulted in a 60% annual growth loss, or a cumulative loss of 34% over the 5-year period. This cumulative growth loss was equivalent to 15 m^3/ha of wood production lost to the stand during 5 years of non-fatal defoliation. Other results from the study showed that plots with a history of defoliation increasing from 20 to 90% of current foliage over 4 or 5 years suffered about a 40% annual growth loss, and that preventing defoliation by spraying with insecticide after several years of defoliation apparently reduced the growth loss, but not by very much (Table 2).

The study by Baskerville and MacLean (1979) also provided data of volume losses on a stand basis. Whereas the stands studied by Kleinschmidt et al. (in press) suffered non-fatal defoliation, the fir plots examined by Baskerville and MacLean (1979) were so severely defoliated in the mid-1950's that from 18 to 80% of the total volume per hectare of the ten plots was killed. Recovery of these stands was studied over 20 years following the collapse of the budworm outbreak. Within five years of the cessation of defoliation, the crowns of surviving trees appeared fully recovered, and diameter and height growth

Table 2. Reduction of volume increment in fir-spruce plots in Maine resulting from varying degrees of non-fatal defoliation (from Kleinschmidt, Baskerville and Solomon, in press)

5-year defoliation history (for fir)	Annual fir growth loss(%) after 5 yrs defoliation	Mean cumulative fir growth loss	
		%	m^3/ha
A. Light (<20%)	No growth loss measurable.		
B. Increasing for 4 years (from roughly 20% to 90%)	40	12	4
C. Increasing for 5 years (from roughly 20% to 90%)	40	19	7.5
D. Severe for 5 years (continuous 90 to 100%)	60	34	15
E. Increasing for 4 years, sprayed in 5th year	55	30	17
F. Increasing for 3 years, sprayed in 4th year	30	18	13

were similar to that in unaffected stands. Diameter growth showed a classic response to the reduction in stand density (thinning) resulting from the budworm-caused mortality, and increased substantially beyond predefoliation levels; this was also noted by Williams (1967). However, the recovery in terms of volume per hectare was poor, because the increased diameter growth was on smaller trees (as a result of the growth reductions during the outbreak) and there were fewer trees per hectare. The decreased height growth (Figure 2) was particularly important because the defoliated trees were 3 to 4 m shorter than similar non-defoliated trees after the outbreak collapsed. Only one of the ten plots had regained its predefoliation volume 15 years after defoliation ceased (Baskerville and MacLean 1979). Projection of stand development to age 75 years further suggested that on average, the plots which suffered budworm-caused mortality and growth loss would have only slightly more than one-half the projected volume without defoliation.

DISCUSSION

Calculation of a "growth loss" resulting from defoliation, either as a percentage or as a volume of wood per tree or per hectare, requires a measure of "potential" growth in the absence of defoliation. This has been considered several ways in past studies. Studies of radial increment loss (Table 1A) calculated the loss by comparing ring widths during the outbreak period with ring widths in the predefoliation period, using data from either 1, 5, or 10 years preceding defoliation. Use of data just one year prior to defoliation is inadvisable because of the variation in annual growth which results from climatic differences. Two of the more recent impact studies (Table 1B) calculated growth loss by comparing defoliated trees or plots with trees or plots that had not suffered damage. Batzer (1973) used a paired plot design and maintained undamaged plots by spraying with insecticide, while Baskerville and MacLean (1979) made comparisons with plots in the study area which suffered only light defoliation. Piene (in press), and Kleinschmidt et al. (in press) calculated growth loss by extrapolating potential volume growth of individual trees from the predefoliation growth performance. In Piene's study, extrapolation was particularly easy because of the growth response of the trees to a spacing treatment carried out five years previously. Of all these methods for determining potential growth, the maintenance of sprayed "control" plots adjacent to the defoliated plots is most desirable, as climate-caused growth differences will thereby be accounted for.

Defoliation definitely results in decreased radial and volume growth of individual trees, and the loss of wood production by forest stands. This is not surprising, because defoliation removes a portion of the tree's photosynthesis apparatus, which is responsible for primary production. Data currently exist to roughly quantify the growth loss resulting from several years of severe defoliation at about 50 to 75% for balsam fir, the major host species. However, it must be emphasized that this is just a rough estimate; few data exist on the magnitude of the growth loss resulting from varying degrees of defoliation, or from different temporal sequences of defoliation (e.g., how does growth loss resulting from several years of moderate defoliation compare with growth loss resulting from defoliation increasing from initially light to finally severe, over a number of years?). Also, no data presently exist on effects of characteristics such as age, stand density, site quality, species composition, or previous stand history on the growth loss of individual trees and stands. Similarly, more data are required to quantify growth loss in host tree species other than balsam fir.

Studies of growth loss resulting from defoliation should consider loss of volume increment of both individual trees and stands. Although useful information about the past history of individual trees can be extracted from radial growth sequences such as those of Duff and Nolan (1953), the use of volume increment data accounts for the natural variability of the internal growth pattern of trees, and thus clarifies effects of external influences, such as defoliation, on tree growth. And although the loss of growth by individual trees is definitely of interest, the stand is the conventional unit of forest management, and more data are required on effects of defoliation at this level.

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