SPRUCE BUDWORM DEFOLIATION IN YOUNG BALSAM FIR: THE 'GREEN' TREE PHENOMENON

HARALD PIENE and ELDON S. EVELEIGH[1]

Canadian Forest Service - Fredericton, PO Box 4000, Fredericton, New Brunswick, Canada E3B 5P7

Abstract

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During a severe outbreak of spruce budworm, *Choristoneura fumiferana* (Clem.), some balsam fir trees, *Abies balsamea* (L.) Mill., remain noticeably greener than others in the same stand. We show that this 'green' tree phenomenon is not caused by differential defoliation in which certain trees experience consistently low defoliation pressure throughout an outbreak. Rather, these trees remain 'green' because of their prolific, epicormic shoot production which is consistently high during an outbreak, giving them a 'greener' appearance than other trees that produce lower numbers of epicormic shoots.

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Résumé

Au cours des épidémies graves de la Tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clem.), certains sapins baumiers, *Abies balsamea* (L.) Mill., restent beaucoup plus verts que d'autres sapins du même peuplement. Ce phénomène n'est pas causé par une défoliation différentielle par laquelle certains arbres subissent une moins grande pression de défoliation que d'autres durant une épidémie. Ces arbres demeurent plus verts surtout à cause de la production plus importante de pousses adventives durant une épidémie, ce qui les rends plus verts que les autres arbres qui produisent moins de pousses adventives.

[Traduit par la Rédaction]

Introduction

During the course of severe outbreaks of spruce budworm, *Choristoneura fumiferana* (Clem.), some balsam fir trees, *Abies balsamea* (L.) Mill., remain noticeably greener than others when viewed from the ground. One frequently proposed explanation for this 'green' tree phenomenon is that certain trees, for unknown reasons, consistently incur lower levels of defoliation than do other trees (i.e. differential defoliation). However, to our knowledge, there are no data to support this explanation. We hypothesize that the phenomenon is explained by more vigorous production of epicormic shoots over time and, hence, more foliar biomass in some trees in response to bud destruction by spruce budworm feeding. In referring to differential growth patterns in balsam fir, McDonald (1981) suggests differences in phenotypes, which lends support to our hypothesis. In our paper, we examine both possible explanations and present field and laboratory data that support our new hypothesis that differential epicormic shoot production accounts for the 'green' tree phenomenon.

Methods

Cape Breton Highlands. Study area and plot establishment. The study area is located in the southern part of the Cape Breton Highlands, Nova Scotia, in an almost pure forest of 20- to 30-year-old balsam fir. Large parts of this forest were spaced in 1971 to 2.4 by 2.4 m (Piene 1981). A severe outbreak of spruce budworm started in the area in 1976 and destroyed most of the current-year foliage. Because the increase in spruce budworm populations in

[1] Population Ecology Group, Department of Forest Resources, University of New Brunswick, Fredericton, New Brunswick, Canada E3B 6C2.

1977 and 1978 was sharp, the current-year foliage was destroyed in the early stages of shoot elongation in both years, accompanied by extensive backfeeding (feeding on older age classes of foliage). After 1978, spruce budworm populations decreased, and only the current-year foliage was defoliated until the spruce budworm populations decreased to low levels in 1983. An exception was in 1980 when backfeeding also occurred on 1-year-old foliage (Piene 1989).

Four 0.025-ha plots, two in a spaced defoliated stand and two in an adjacent unspaced defoliated stand, were established in 1976. These plots were part of a larger study relating spruce budworm defoliation to growth loss in young balsam fir (Piene et al. 1981).

Defoliation measurements. A subset of trees, representing the range of diameters present, was selected in each plot. Defoliation for each year was estimated on these trees in the spring of the following year, before spruce budworm feeding began. To account for variability in defoliation with tree height and aspect, one branch from each whorl was selected, starting from the top of the tree and continuing in a spiral down the tree, covering approximately the upper 85% of the crown. The same branches were examined each year using each second-order branch (laterals growing from the main branch axis) as a discrete sampling unit.

From 1976 to 1978, damage to each age class of needles was visually estimated along the mid-rib of each second-order branch sampled; visual examination of individual shoots has been shown to be an accurate method for estimating defoliation (MacLean and Morgan 1981). In 1976, defoliation was estimated in 10% classes. However, based on the experience from 1976, it proved difficult to assess defoliation in these narrow classes and, in 1977 and 1978, the defoliation classes were expanded to include only seven classes: 0–20, 21–40, 41–60, 61–80, 81–99, 100%, and destroyed shoots. After 1978, the 0–20% class was subdivided into 0–10 and 11–20% classes. The current-year foliage was completely destroyed by the spruce budworm in the early stages of shoot elongation in 1977 and 1978, causing prolific production of epicormic buds. A decrease in spruce budworm populations in 1979 allowed these buds to develop into shoots and, on a number of trees, some branches had as many as 300–800 shoots. This prolific shoot production altered the regular growth pattern of the branches. Therefore, the sampling effort was increased, and defoliation of post-1978 foliage was estimated for each shoot on the second-order branches each year.

Average defoliation for each age class of needles on a branch was calculated based on a weighted mean procedure: the number of shoots in each defoliation class was multiplied by the mid-point of its defoliation class, summed, and divided by the total number of shoots sampled. Based on data from 1977 to 1979, defoliation could be estimated within 4% of the mean by sampling every second branch (Piene et al. 1981). This sampling procedure was adopted after 1979. For further details see Piene (1989). The number of current-year shoots was counted on each sample branch from 1979 to 1984.

Acadia Forest Experiment Station. Study area. The study area, Red Pine Brook, located at the Acadia Forest Experiment Station near Fredericton, New Brunswick, consisted of approximately 98% 35- to 40-year-old balsam fir (Lethiecq and Régnière 1988). An outbreak of spruce budworm started in the area in the late 1970s, reached its peak in 1985, and began to decline in 1986. From 1981 to 1989, the spruce budworm population in this stand was sampled intensively as part of a large study on the population dynamics of this pest.

In 1983, a few, relatively 'greener' and 'fuller' trees were noticed in the stand. Prior to emergence of the spruce budworm in the spring of 1984, three of these 'green' trees were visually selected (hereafter referred to as 'green' trees A, B, and C) for comparison with 20 other trees that were more grey-green in appearance, presumably because of severe defoliation (hereafter referred to as 'grey' trees). To determine if the 'green' tree appearance could be explained by consistently lower densities of spruce budworm, pupae and egg masses on the 23 trees were sampled at the occurrence of peak pupae and after most of the eggs had hatched in 1984 and 1985. One whole, mid-crown branch was removed from each tree, the branch surface area was estimated from length and width measurements, and the number of living pupae and egg masses per square metre of foliage was calculated for each tree.

A laboratory experiment was conducted to determine if the 'green' appearance was the result of lower survival of spruce budworm from the larval to adult stage on the 'green' trees than on the 'grey' trees. Sixty fourth-instar larvae were randomly collected in 1984 from branches removed from the trees: 30 larvae from the 'green' trees, and 30 from the 'grey' trees. An equal number of larvae (15) from each group of trees was reared individually on foliage collected from the 'green' and 'grey' trees in a 2 by 2 design. The foliage was placed in vials of water and sprayed with water once each day. Foliage was replenished as required and the fate of larvae was recorded daily. Of the 60 larvae, 56 remained for analysis; one larva was not a spruce budworm, and three larvae escaped during the experiment.

Data Analyses. Based on the average defoliation level of each tree in Nova Scotia in 1976, two groups of trees were established in each of the spaced and unspaced stands. One group consisted of five trees with the least defoliation; the remaining trees formed the other group (hereafter termed low and high defoliation groups). Similarly, based on the ranking of average number of shoots produced by each tree in 1979, two other groups of trees (hereafter termed low and high epicormic shoot producers) with similar diameter at breast height, crown length and width were established in each of the spaced and unspaced stands. Average differences between groups in percentage defoliation from 1976 to 1984, and in shoot production from 1979 to 1984, were analyzed using a Kruskal-Wallis test with a 0.05 level of significance.

Differences in survival of spruce budworm larvae reared on foliage from the 'green' and 'grey' trees were analyzed with the 2 by 2 test of independence, using the *G*-statistic (Sokal and Rohlf 1981) with a 0.05 level of significance.

Results and Discussion

Differential Defoliation. If certain trees look 'green' because of consistently lower defoliation levels, the significant difference in defoliation between the high and low defoliation groups selected in 1976 (Table 1) should remain throughout the spruce budworm outbreak. However, from 1977 to 1984, there was no significant difference in the average percentage defoliation between the groups that had the high and low defoliation in 1976 in either the spaced or unspaced stands each year (Table 1). This indicates that trees with the least defoliation in 1976 did not continue to have the least defoliation in the following years of the outbreak. This is also illustrated in Figure 1 in which trees with the lowest amounts of defoliation in any year are tracked for subsequent changes in defoliation levels for the following years. Characteristically, the trees that were the least defoliated within a given year were never the least defoliated the next year. In fact, one tree had the least defoliation of all one year, but the most the next year (Fig. 1, spaced trees, 1979–1980).

Also, if certain trees were 'green' because of lower amounts of defoliation, then one would expect that spruce budworm densities would be lower on these trees because female moths either avoided ovipositing on these trees, or larvae survived poorly, or both. However, pupal and egg mass populations on the 'green' and 'grey' trees indicate that the 'green' trees were as susceptible to spruce budworm attack as the 'grey' ones (Table 2). With the exception of the low number of egg masses on 'green' tree A and the very high number of egg masses on 'green' tree C in 1985, the numbers of pupae and egg masses on the 'green' trees all fell within the corresponding ranges for the 'grey' trees in 1984 and 1985. Therefore, female spruce budworm did not avoid ovipositing on the 'green' trees. Furthermore, the laboratory feeding experiment indicated no significant difference in the survival of spruce budworm larvae reared on foliage from 'green' versus 'grey' trees: 75.9% (22 of 29) of the larvae

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TABLE 1. Average percentage defoliation for two groups of spaced and unspaced balsam fir trees from 1976 to 1984 in Nova Scotia. The two groups were selected in 1976; one group (Low) consisted of five trees with the lowest defoliation in 1976, and the remaining trees formed the other group (High). See Methods

	% defoliation									
	Spaced					Unspaced				
Year	*N**	High	*N*	Low	χ^{2}†	*N*	High	*N*	Low	χ^2
1976	12	90.8(2.1)‡	5	68.0(3.4)	10.0§	13	93.6(1.5)	5	69.7(8.6)	10.3§
1977	12	240.8(7.5)‖	5	244.7(7.6)	0.9	13	209.2(9.7)	5	220.1(19.7)	0.1
1978	12	148.7(4.9)	5	159.1(8.8)	1.9	13	146.7(6.6)	5	149.9(7.2)	0.1
1979	12	79.6(2.4)	5	75.8(4.5)	0.5	13	79.5(3.6)	5	80.9(4.7)	0.0
1980	12	111.3(3.4)	5	110.2(4.0)	0.2	13	105.5(4.0)	5	108.1(5.3)	0.0
1981	10	79.2(4.7)	4	70.7(8.6)	—¶	13	64.9(4.1)	5	68.3(5.4)	0.9
1982	8	32.5(10.3)	3	31.7(7.2)	—	11	34.8(4.5)	5	41.8(6.3)	0.5
1983	6	26.5(10.0)	2	18.0(3.0)	—	11	35.8(6.2)	5	30.1(8.9)	0.5
1984	5	10.9(2.9)	2	23.2(12.5)	—	10	10.9(1.5)	5	15.3(6.5)	0.0

* *N* = number of trees.
† χ^2 = Kruskal-Wallis (chi-square).
‡ Standard error.
§ Significant difference, $P = 0.05$.
‖ Because defoliation was measured on several foliage age classes, total defoliation was obtained by summing the defoliation of the individual age classes. This resulted in values over 100% in some cases.
¶ No statistical tests were performed because of too few trees (loss resulting from tree mortality).

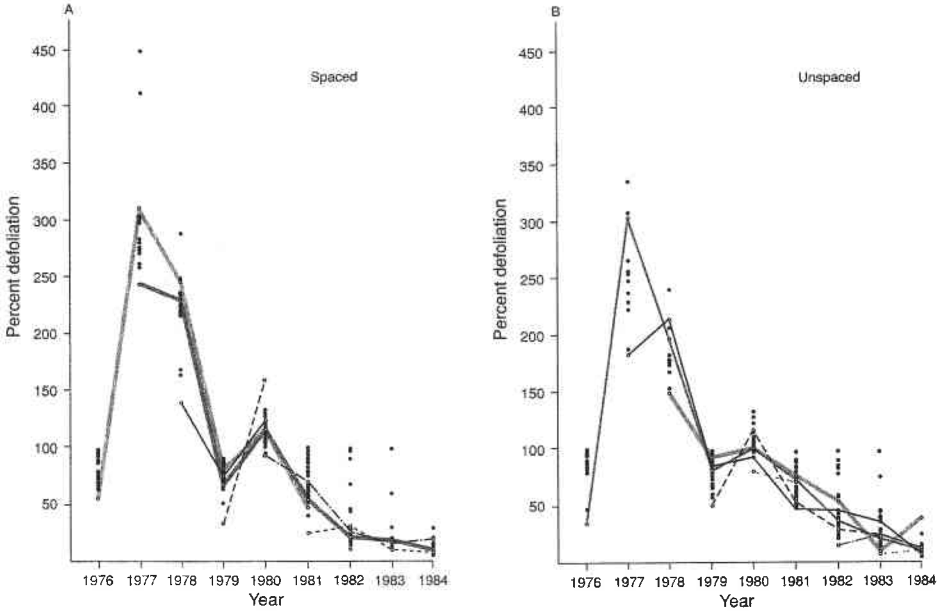

FIG. 1. Changes in average percentage defoliation for all (A) spaced and (B) unspaced sample trees from 1976 to 1984. As defoliation was estimated on a number of age classes for each tree, percentage defoliation was obtained by summing the defoliation for each age class, thus exceeding 100% for some years. The lines follow individual trees that in a particular year had the lowest percentage defoliation. Because of tree mortality, certain trees could not be followed throughout the spruce budworm outbreak (adapted from Piene 1989).

reared on 'green' tree foliage survived to the adult stage, and 55.6% (15 of 27) survived on foliage from the 'grey' trees ($G = 2.92, P > 0.05$). A significantly lower rate of larval survival on the 'green' trees would be expected if the 'green' trees were 'greener' because of poor survival of feeding larvae.

To summarize, our data do not support the hypothesis that 'green' trees occur during a spruce budworm outbreak because they experience consistently lower defoliation levels as a result of lower densities of spruce budworm.

TABLE 2. Number of spruce budworm pupae per square metre of foliage at peak pupal population level and number of egg masses per square metre when most eggs had hatched on 'green' and 'grey' balsam fir trees in the Acadia study area, New Brunswick, in 1984 and 1985

	1984		1985	
Tree condition	No. or mean no. of pupae	No. or mean no. of egg masses	No. or mean no. of pupae	No. or mean no. of egg masses
'Green'				
A	121	62	200	37
B	133	179	108	507
C	147	200	279	708
'Grey'	180*	287	230	256
$N = 20$	(96–311)†	(43–540)	(56–526)	(56–635)

* Mean.
† Range.

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TABLE 3. Average number of shoots per branch and percentage defoliation for two groups of spaced and unspaced balsam fir trees from 1979 to 1984 in Nova Scotia. The selection of the two groups (high and low epicormic shoot producers) was made in 1979 based on ranking the trees from the highest to the lowest shoot producers. See Methods

	Spaced									Unspaced							
	No. of shoots					% defoliation			No. of shoots					% defoliation		
Year	N*	High	N	Low	χ^2†	High	Low	χ^2	N	High	N	Low	χ^2	High	Low	χ^2
1979	11	137.7(11.7)	12	64.8(6.0)‡	16.5§	74.3(2.7)	81.3(2.1)	3.6	13	76.3(6.2)	9	27.6(3.2)	15.3§	81.0(3.2)	81.3(4.7)	0.0
1980	11	247.1(29.3)	12	180.5(16.9)	3.4	114.0(3.0)‖	114.0(3.8)	0.2	13	158.1(17.2)	9	71.4(12.0)	10.1§	107.6(2.8)	99.3(5.4)	0.6
1981	11	167.8(44.3)	10	77.8(23.1)	2.6	73.9(5.8)	73.5(7.9)	0.1	13	101.9(18.0)	9	40.8(6.7)	10.5§	64.2(4.7)	69.9(3.6)	1.5
1982	10	196.3(60.3)	6	78.2(20.4)	1.7	27.9(5.3)	56.6(14.2)	3.8	13	102.9(15.8)	8	44.6(4.9)	8.4§	39.1(4.2)	33.0(4.6)	1.3
1983	9	129.4(43.5)	3	107.9(28.6)	—	37.0(10.6)	11.0(2.9)	—	13	84.8(12.7)	8	43.5(8.2)	5.9§	31.2(5.2)	31.6(8.5)	0.0
1984	7	166.0(48.0)	2	113.8(11.2)	—	12.2(3.9)	14.3(8.2)	—	13	71.1(10.9)	8	43.8(15.7)	2.8	12.3(2.2)	16.6(5.4)	0.2

* N = number of trees; the decreasing number as time went on, especially for the "low" spaced group, is a result of tree mortality. Because of the low number of spaced trees in the "low" group in 1983–1984, no statistical test was performed.
† χ^2 = Kruskal-Wallis (chi-square).
‡ Standard error.
§ Significant difference, $P = 0.05$.
‖ Because backfeeding occurred on 1-year-old foliage in 1980, defoliation was obtained by summing the defoliation for current and 1-year-old foliage resulting in values over 100% in some cases.

Shoot Production. After 3 years (1976–1978) of severe defoliation in the Cape Breton Highlands study area, which included 2 years of complete destruction of the current-year foliage and extensive backfeeding, the trees looked uniformly grey-brown in the spring of 1979. As the spruce budworm populations decreased from 1979 onward, all the spaced and unspaced trees started to refoliate with shoot production varying greatly among trees. The unspaced trees that were classified as high shoot producers in 1979 continued to produce a significantly higher number of shoots than did the low shoot producers (about twice as many shoots) each year from 1980 to 1983 (Table 3). The same trend was apparent in the spaced trees, but there was no significant difference in shoot production between the high and low group (Table 3). This was because of exceptionally large variability in shoot production among the spaced trees, primarily because certain trees became weakened, produced very low numbers of shoots, and eventually died. As a result of the accumulated higher production of shoots over time, the trees in the high shoot-producing group looked conspicuously 'greener' than the trees in the low group in both the spaced and unspaced stands. It is important to emphasize that this 'greener' appearance is the result of a consistently higher shoot production, and not of lesser defoliation pressure, because there was no significant difference in defoliation between the trees in the high and low shoot-production groups for either the spaced or unspaced stand (Table 3).

Conclusion

Our results show that certain balsam fir trees maintain a 'greener' appearance during an outbreak of spruce budworm because of their consistently greater production of epicormic shoots than that of other trees that appear 'greyer', and not because of consistently lower defoliation pressure. Thus, silvicultural programs should concentrate on those trees that exhibit high shoot production because they are more likely to survive severe outbreaks of spruce budworm (Piene 1989).

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