Deterioration of severely defoliated balsam fir in relation to stand age, spacing, and foliar protection

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Balsam fir (*Abies balsamea* (L.) Mill.) trees that had been heavily defoliated by the spruce budworm (*Choristoneura fumiferana* (Clem.) were felled and examined for decays and secondary insect activity during the declining phase of the budworm outbreak. Trees were sampled in (*i*) a 25- to 30-year-old stand that had been spaced a decade earlier to about 2.4 × 2.4 m and allowed to become defoliated, (*ii*) adjacent unspaced controls, (*iii*) a nearby mature (60- to 80-year-old) stand that had been defoliated, and (*iv*) and (*v*) spaced and unspaced plots that had been protected from defoliation by annual sprays of trichlorfon. Sampling was done annually over a 4-year period from preselected defoliated trees, and after the budworm population had collapsed from trees that had been intensively studied with respect to defoliation and mortality. Where defoliation was allowed to proceed unchecked (*i*) one-half of the spaced, (*ii*) one-third of the unspaced, and (*iii*) all of the mature trees died. The trees were attacked by wood wasps (Siricidae) and the sapwood-staining fungus, *Amylostereum chailletii* (Pers. ex Fr.) Boidin, followed by various stem-invading insects (*Pissodes dubius* Rand., *Pityokteines sparsus* Lec., *Trypodendron lineatum* (Oliv.), and *Monochamus scutellatus* Say) and by the sap-rot fungus *Hirschioporus abietinus* (Pers. ex Fr.) Donk. In surviving defoliated trees (*i* and *ii*) and in trees that had been protected by trichlorfon sprays (*iv* and *v*), numerous siricid injuries with associated pockets of stain caused by *A. chailletii* were found in the lower bole.

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Des Sapins baumiers (*Abies balsamea* (L.) Mill.) qui avaient été sévèrement défoliés par la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.) ont été abattus et examinés quant à la présence de caries et d'activités d'insectes secondaires pendant la phase du déclin de l'épidémie de tordeuse. Ces sujets de sapin ont été échantillonnés dans (*i*) un peuplement âgé de 25 à 30 ans qui avait été éclairci une décennie auparavant à un espacement de 2,4 sur 2,4 m et qui avait subi par la suite une défoliation, (*ii*) des témoins adjacents non éclaircis, (*iii*) un peuplement voisin mûr (âgé de 60 à 80 ans) qui avait été défolié, ainsi que (*iv*) et (*v*) des places d'étude éclaircies et non éclaircies qui avaient été protégées de la défoliation au moyen de pulvérisations annuelles de trichlorfon. L'échantillonnage a été fait annuellement durant une période de 4 ans à partir de sujets défoliés préalablement choisis et, une fois que les populations de tordeuse se furent effondrées, à partir des sujets qui avaient été intensivement étudiés quant à la défoliation et à la mortalité. Là où la défoliation a pu se faire sans entrave, la moitié des sujets éclaircis (*i*), le tiers de ceux non éclaircis (*ii*) et tous les arbres mûrs (*iii*) sont morts et ont été attaqués par les guêpes du bois (Siricidées) et par le Champignon de décoloration de l'aubier, *Amylostereum chailletii* (Pers. ex Fr.) Boidin, suivie de divers insectes envahisseurs du tronc (*Pissodes dubius* Rand., *Pityokteines sparsus* Lec., *Trypodendron lineatum* (Oliv.) et *Monochamus scutellatus* Say) et par le Champignon de carie de l'aubier *Hirschioporus abietinus* (Pers. ex Fr.) Donk. Chez les sujets défoliés survivants (*i* et *ii*) et chez les sujets qui avaient été protégés au moyen de pulvérisations au trichlorfon (*iv* et *v*), plusieurs dommages causés par les siricides, de même que des plages de décoloration causées par l'*A. chailletii* et qui leur étaient associés, ont été trouvés dans la partie inférieure du tronc.

[Traduit par la revue]

Introduction

Increasing demands on the forest resource and expectations of future timber deficits have caused increased attention to the young, regenerating forest (Reed and Associates, Ltd. 1978). Over the past two decades, investments in silvicultural programs such as spacing of young stands have been made with expectations of increased yields, shorter rotations, and avoidance of the numerous insect and disease problems associated with the old forest. Nevertheless, insects and diseases are exerting considerable pressures on young managed forests (Gibson 1974; Powers et al. 1974; Whitney et al. 1983) and consequent losses are in most cases difficult to predict. As a result, there are few reliable guidelines whereby future yields of sound, merchantable wood can be determined for the new forest.

The spruce budworm (*Choristoneura fumiferana* (Clem.)) is one of the major limitations to forest productivity in eastern North America. In the past 100 years, three major outbreaks have occurred, the most recent beginning in the late 1960s and reaching a peak in the Atlantic Provinces in the mid-1970s. The resulting losses in the spruce–fir forests, together with increased demands for softwood fiber, have raised doubts that future wood supply demands can be met (Reed and Associates, Ltd. 1978).

A major consideration in predicting losses to the spruce budworm is the salvageability of severely defoliated and dead trees. Losses to decay, reduction in pulp quality, increased harvesting and storage costs, and distorted supply–demand ratios must be assessed (Basham 1984). The subject of mortality and deterioration of budworm-damaged fir has been studied extensively (Basham 1959; Basham and Belyea 1960; Basham et al. 1976; Belyea 1952; Shortle and Ostrofsky 1983; Stillwell and Kelly 1964). Decay susceptibil-

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ity increases in defoliated trees (Shortle and Ostrofsky 1983) but the actual onset of sapwood decay has been observed only after the trees have died (Basham 1959). Wood wasps of the family Siricidae are very important in the early stages of stem deterioration as vectors of *Amylostereum chailletii* (Pers. ex Fr.) Boidin, the fungus usually causing stain and incipient decay (Stillwell 1960). Wood wasps are capable of attacking weakened living trees, as well as those recently killed (Stillwell 1966). Bark beetles, notably *Pityokteines sparsus* Lec., attack recently killed fir trees and are especially common in the Great Lakes Region (Basham 1986). Also important in the early stages of deterioration are the weevils (*Pissodes dubius* Rand.), long-horned borers (*Monochamus* spp.), ambrosia beetles (*Trypodendron lineatum* (Oliv.), the wood-rotting fungus *Stereum sanguinolentum* (Alb. and Schw. ex Fr.) Fr., and numerous Fungi Imperfecti (Basham 1959; Belyea 1952). Root- and butt-rot fungi, especially *Armillaria mellea* (Vahl. ex Fr.) Kummer, may hasten the death of defoliated trees (Stillwell and Kelly 1964). The advanced stages of stem deterioration, critical in salvage of killed stands, have been found to be mainly white pitted sap rot caused by *Hirschioporus abietinus* (Pers. ex Fr.) Donk (Basham 1959). Regional differences in the pattern of stem deterioration are reported in Basham et al. (1976).

Most previous investigations were conducted in mature balsam fir stands which had developed with minimal human intervention. Information on the deterioration of fir in young, managed stands after severe defoliation is now needed. In the Cape Breton Highlands of Nova Scotia, a sizable investment was made in the cleaning and spacing of dense balsam fir regeneration (Axelsson and Routledge 1970), and a significant growth response was noted (Piene 1981). A sudden and severe outbreak of spruce budworm on Cape Breton Island caused extensive mortality in the mature fir and threatened the young, spaced stands (Branch 1981; MacLean 1979; Magasi 1978; Ostaff 1982; Piene 1980; Sterner et al. 1977). The extent of mortality and the pattern of deterioration of weakened and dead trees in the young, spaced stands were largely unknown.

The objectives of this study were to follow the course of stem deterioration in young spaced trees subjected to severe defoliation, and to compare the deterioration pattern with that in mature balsam fir, unspaced young stands, and stands that had been protected from defoliation with insecticides. This was done in order to understand better the effects of stand treatment on deterioration after severe budworm damage.

Materials and methods

The study area and experimental design

This investigation was part of a larger study at Crowdis Mountain, Cape Breton Highlands, Nova Scotia, details of which are given by Piene et al. (1981). The stands in which this study was undertaken are almost pure balsam fir and are part of the Cape Breton Highlands ecoregion (Loucks 1959–1960). These were clear-cut in the mid-1960s, leaving small pockets of residual fir which had originated in the early part of the century. Dense fir regeneration which occupied most of the clear-cuts was spaced in 1971 to about 2.4 × 2.4 m. A more detailed description of the study area and early effects of spacing are given by Piene (1981). Some of the early effects of the budworm epidemic, which began in 1976 in the study area, are reported by Piene (1980).

The experimental design is described by Piene et al. (1981). Eight 0.025-ha plots, within 300 m of each other on similar sites, were established in 1976. Four of these had been spaced to 2.4 × 2.4 m in 1971 and four had been left unspaced at densities of 20 000 – 60 000 stems/ha. Two spaced and two unspaced plots were protected from defoliation by annual applications of trichlorfon (Dylox®, Chemagro Chemical Co. Ltd., Toronto, Ontario) each spring before larval feeding began. Insecticide application in these protected (P) plots was begun in 1977 and was discontinued in 1984 after the budworm population had collapsed. The remaining (D) plots were allowed to be defoliated each year throughout the budworm epidemic.

Successive changes in deterioration of defoliated trees

In 1980, at which stage the balsam fir in the area had undergone complete defoliation for 4 years but very little mortality was yet evident, 150 codominant trees were selected and numbered in the vicinity of the D plots. Fifty of these were in the young, spaced stand, 50 in the unspaced controls, and 50 from a nearby 60- to 80-year-old mature (M) stand of balsam fir. In the autumns of 1980, 1981, and 1982 ten trees were selected at random from each of the above categories and felled for deterioration studies. In the autumn of 1983, the remaining 20 trees in each category were harvested.

Trees were dissected and examined immediately after felling. If the cambium was dry and discolored throughout the stem, they were recorded as dead. Stems were sectioned into 1-m bolts from the stump (about 5 cm high) to the terminal shoot. From the base of each bolt, a 5 cm long disk was cut for decay studies. The remainder of each bolt was then examined for evidence of secondary insect activity. This was done by peeling first to the phloem to find the small reddish lesions associated with woodwasp oviposition and the brood chambers of bark beetles and weevils. The remainder of the bark was then removed in search of the entrance and emergence holes made by various insects. Evidence of each type of insect activity was recorded for each 1-m bolt.

The 5-cm disks for decay studies were stored at −2°C when not in transit. Within 2 weeks after collecting, they were examined and cultured for decay and stain fungi. For each disk, the diameter inside bark was recorded and the cross-sectional area of each pocket of decay or stain determined by planimetry using a Calcomp 2000 digitizer tablet. Stem diameters and cross-sectional areas of each type of decay or stain were plotted on height–area graphs from which volumes were calculated using the digitizer. Decays and stains were classified as (*i*) firm light brown to orange-brown sapwood stain or incipient decay as described by Basham (1959) and Stillwell (1960), (*ii*) advanced sap rot which could be removed by tangential pressure from the thumb and forefinger, (*iii*) heart rots which occupied the central part of the stem above the lowermost bolt, and (*iv*) butt rots, which occupied the central part of the stump and lowermost bolt.

Microorganisms associated with each type of decay and stain were cultured from each disk. Disks were dipped in 3% Dettol solution, split longitudinally through the decay pocket, and three small (ca. 2 × 2 × 5 mm) chips were removed aseptically and placed on 2% malt agar in 9-cm Petri dishes. Petri dish cultures were incubated under normal laboratory conditions. The microorganisms growing from the chips were classified according to mycelial, spore, and mat characteristics. The most frequently occurring types were identified with the assistance of personnel at the Biosystematics Research Centre, Agriculture Canada, Ottawa. Nomenclature of wood-rotting Basidiomycetes was that of Stalpers (1978).

Deterioration of trees with known defoliation–mortality histories

In each of the plots described in the section entitled "The study area and experimental design," a subset of 10 to 25 representative trees was selected at the beginning of the budworm epidemic for intensive annual study of defoliation (Peine et al. 1981). In the autumn of 1984 and the summer of 1985, after the budworm epidemic had collapsed, these trees were harvested for studies of

TABLE 1. Mortality of defoliated balsam fir and occurrence of secondary stem insects and decays over a 4 year period at Crowdis Mountain, Cape Breton Highlands, Nova Scotia

Type of damage and years observed	No. of dead trees			No. of living trees		
	Mature	Spaced	Unspaced	Mature	Spaced	Unspaced
Total sample						
1980	1	0	0	9	10	10
1981	6	0	0	4	10	10
1982	6	0	3	4	10	7
1983*	17	10	6	3	10	14
Damaged by Siricidae†						
1980	0	—	—	0	0	1
1981	0	—	—	3	2	1
1982	1	—	1	1	0	2
1983*	8	4	4	3	8	7
Damaged by *Trypodendron lineatum*						
1983*‡	5	4	2	1	0	0
Damaged by *Pityokteines sparsus*						
1983*‡	2	1	0	0	0	0
Damaged by *Pissodes dubius*						
1983*‡	9	8	2	1	0	3
Damaged by *Monochamus* spp. §						
1983*‡	10	4	2	0	0	0
Sap stain and incipient sap rot						
1980	1	—	—	0	1	2
1981	6	—	—	2	1	0
1982	6	—	3	2	2	2
1983*	17	10	6	3	5	7
Advanced sap rot						
1981‡	2	—	—	0	0	0
1982	3	—	0	0	0	0
1983*	14	8	3	0	0	0

*Twenty trees in each of the three groups (mature, spaced, and unspaced), rather than 10 as in the previous 3 years.
†*Urocerus albicornis* F. adults found in vicinity of plots.
‡Not observed in previous years.
§*Monochamus scutellatus* Say adults found in vicinity of plots.

deterioration. The stems were sectioned at every third internode and disks for decay studies were collected from the base of each bolt, as described in the previous section. Bolts were peeled and examined for evidence of secondary insect activity in the same manner as described above, except that counts were made of oviposition holes, brood galleries, and emergence holes and expressed in terms of density per unit of stem surface area. Decay volumes and culturing of decay and stain fungi were treated in the same manner.

Results

Successive changes in deterioration of defoliated trees

Sampling of trees adjacent to the defoliated plots in the autumn months of 1980, 1981, 1982, and 1983 showed annual increases in incidence of dead trees and injuries by siricid wood wasps, ambrosia beetles (*Trypodendron lineatum*), bark beetles (*Pityokteines sparsus*), weevils (*Pissodes dubius*), and sawyer beetles (*Monochamus* spp.), as well as decays (Table 1). No tree mortality was recorded in the sample of young, spaced trees until 1983. Bark beetle and sawyer beetle damage and advanced sap rots were found only in dead trees while wood wasp oviposition holes, ambrosia tunnels, weevil galleries, and pockets of sap stain and incipient sap rot could be found in both living and dead trees. Prior to 1983, wood wasp oviposition holes were the only evidence of secondary stem insect activity detected.

Mean volumes and percentages of stained and decayed wood for the 4-year sample period are shown in Table 2. The proportion of sapwood stain or incipient decay was greatest in the mature stand and did not reach appreciable levels in the young stands, spaced or unspaced, until 1983. The proportion of advanced sap rot was greatest in the spaced trees.

The incidence and percentage of heart rots and butt rots appeared unrelated to mortality, age, treatment, or year of sampling (Table 2). Red heart rot occurred in 11% of the sample trees while butt rots of various colors and consistencies were found in 23% of the 150 trees.

Deterioration of trees with known defoliation–mortality histories

The intensively studied trees in the D and P plots were harvested and dissected in autumn 1984 and summer 1985. Results are summarized in Tables 3 and 4.

Small pockets or longitudinal streaks of firm light brown sap stain associated with wood wasp oviposition holes were found in most of the living trees, mainly in that part of the stem immediately below the crown. *Amylostereum chailletii* usually was cultured from these streaks. Dead trees typically had continuous columns of firm light brown sap stain or incipient decay, extending 1–2 cm inward from the xylem–phloem interface. *Amylostereum chailletii* was again the main fungus isolated. Galleries of ambrosia beetles, bark beetles, and sawyer beetles as well as emergence holes of

TABLE 2. Mean volumes and percentage of total volume of decayed and stained wood in the 1980–1983 samples of balsam fir harvested at Crowdis Mountain, Cape Breton Highlands, Nova Scotia

Stand history and type of defect	1980	1981	1982	1983
Mature				
Total volume, cm^3	79 682	52 268	67 072	53 419
Heart and butt rots, %	0.3	1.1	3.8	1.1
Sap stain and incipient rot, %	1.7	10.9	12.8	25.6
Advanced sap rot, %	0.0	0.0	0.0	3.5
Total stain and decay, %	2.0	12.0	16.7	30.2
Spaced				
Total volume, cm^3	14 988	17 216	18 320	16 477
Heart and butt rots, %	0.1	0.3	0.0	0.4
Sap stain and incipient rot, %	0.7	0.1	0.1	18.8
Advanced sap rot, %	0.0	0.0	0.0	7.8
Total stain and decay, %	0.8	0.4	0.1	27.0
Unspaced				
Total volume, cm^3	10 224	11 280	14 480	11 814
Heart and butt rots, %	0.7	0.3	0.3	0.3
Sap stain and incipient rot, %	0.5	0.0	4.3	13.3
Advanced sap rot, %	0.0	0.0	0.0	2.0
Total stain and decay, %	1.2	0.3	4.7	15.5

siricid wood wasps were found only in dead trees (Table 3). Evidence of ambrosia beetles and *Pityokteines* bark beetles was found in the spaced but not in the unspaced plots. The greater number of wood wasp oviposition scars found in living than in dead trees (Table 3) could be a real difference or it could reflect a difference in ease of detection, i.e., in living trees a distinct reddish bark lesion is formed around the oviposition hole and this is unlikely to develop in dead or dying trees. In the living trees, no wood wasp larval tunnels could be found and the oviposition holes had been overgrown by subsequent cambial activity.

Trees that had been dead 2 years or longer at the time of harvest (deterioration classes 9, 10, and 11) were found only in the spaced D plots (Table 4). Advanced sap rot was present in all of these trees. There was no evidence of *Pityokteines* bark beetle activity in these trees, suggesting that the population had increased in this area after 1982. Cultures from advanced sap rot yielded *Hirschioporus abietinus* plus a wide variety of miscellaneous organisms and *H. abietinus* was fruiting on some of these trees at the time of harvest.

There were few differences between surviving trees in the D plots and the trees harvested from the P plots. The former had slightly more sap rot (Table 4). Also dead tops were present in the surviving D trees but not in the P plots.

Effects of season of mortality on the pattern of deterioration were difficult to determine from the small samples available. Weevil (*Pissodes dubius*) activity peaked in trees that died between September 1983 and June 1984 (Table 3).

Microorganisms associated with decay

Results of isolation attempts from decayed and stained wood are shown in Table 5. Most of the isolation attempts were from firm light brown to orange-brown sapwood stain or incipient decay associated with wood wasp oviposition holes and these gave rise mainly to *Amylostereum chailletii*. However, other organisms were isolated with sufficient frequency from this type of defect to be noted, namely *Stereum sanguinolentum*, *Tyromyces caesius* (Schrad ex Fr.) Murr., *Cytospora* sp., *Pesotum piceae* Crane and Schoknecht, and a slow-growing *Verticillium* sp.

Hirschioporus abietinus was cultured only from trees with advanced sap rot. A blue stain often associated with advanced sap rot and with ambrosia beetle tunnels gave rise to numerous Fungi Imperfecti, including *Pesotum piceae*. Heart rots, as noted in previous studies of balsam fir decay, yielded mainly *Stereum sanguinolentum* in culture. A variety of fungi were cultured from butt rots, including the previously reported species *Coniophora puteana* (Schum ex. Fr.) Karst., *Perenniporia subacida* (Peck) Donk, and *Resinicium bicolor* (Alb. and Schw. ex Fr.) (Basham et al. 1953). The few isolation attempts from dead tops yielded mostly sterile cultures.

Discussion

Young, spaced balsam fir deteriorated rapidly after death caused by defoliation. The apparently rapid rate of deterioration in young spaced trees compared with mature trees is due mainly to smaller diameters and approximately equal radial penetration of sap rot fungi. However, several other factors may be taken into consideration. First, previous mortality of extensive acreages of mature balsam fir on the Cape Breton Highlands probably resulted in a buildup of large populations of secondary stem insects, including wood wasps (D. Ostaff, unpublished data). As a result of massive wood wasp attack on defoliated but still living trees, most of the young trees had numerous pockets of infection by *Amylostereum chailletii* at the time of tree death. The initial stages of sapwood decay were therefore in place at the time of death.

Although most of the secondary insects and fungi encountered in this study were important to some extent in the deterioration of dead trees there is no indication that any were direct causes of death. Bark beetles, often the cause of death of weakened trees in other coniferous species,

TABLE 3. Injuries by secondary stem insects to sample trees with known defoliation histories and dates of mortality

Treatment and deterioration class*	No. of trees	Insect injuries/dm^2 (SD)					
		Siricid oviposition	Siricid exit	*Trypodendron* galleries	*Pityokteines* galleries	*Pissodes* galleries	*Monochamus* galleries
Defoliated, spaced							
9	1						
10	4		0.005	0.041		0.003	
			(0.010)	(0.082)		(0.006)	
11	6	0.027	0.145	0.030		0.214	0.045
		(0.066)	(0.182)	(0.053)		(0.181)	(0.058)
12	3		0.026	0.161	0.073	0.117	0.037
			(0.044)	(0.279)	(0.126)	(0.174)	(0.063)
14	3	0.052				0.425	0.109
		(0.090)				(0.245)	(0.100)
15	4	0.430	0.005		0.229	0.345	0.022
		(0.390)	(0.011)		(0.237)	(0.098)	(0.027)
16	15	0.402				0.017	
		(0.629)				(0.064)	
Defoliated, unspaced							
12	6	0.086				0.015	0.015
		(0.072)				(0.036)	(0.038)
14	3	0.092	0.056			0.391	
		(0.120)	(0.098)			(0.430)	
15	1	0.450				0.019	
16	28	0.826				0.005	
		(0.403)				(0.019)	
Protected, spaced							
16	24	0.356					
		(0.481)					
Protected, unspaced							
16	20	0.297					
		(0.279)					

*Deterioration classes: died June–September 1981 (9); September 1981 – June 1982 (10); June–September 1982 (11); September 1982 – June 1983 (12); June–September 1983 (13); September 1983 – June 1984 (14); June–September 1984 (15); living in September 1984 (16).

appeared only after the trees had died. *Armillaria mellea*, a well-known cause of mortality in stands of trees weakened by defoliation, has been noted on the Cape Breton Highlands (Ostaff 1983) but was not found in plots used in this study. The pattern of deterioration in our study plots appears to have been as follows: defoliation → attack by wood wasps and infection by *Amylostereum chailletii* → compartmentalization of wood wasp and *A. chailletii* injuries → tree mortality → spread of *A. chailletii* throughout the bole → attack by other secondary insects and fungi. In some trees, the compartmentalization of pockets of sapwood infected by *A. chailletii* may have been weak, making a clear separation of cause and effect difficult. However, the high density of wood wasp oviposition punctures and associated compartmentalized pockets of stained sapwood in surviving trees suggest that this is an unlikely cause of tree mortality.

Mortality started later and was lower in the young defoliated stand than in the nearby mature stand. The latter followed closely the pattern observed elsewhere on the Cape Breton Highlands (Ostaff 1982). There is no indication that defoliation pressure was any greater in the mature stand than in the young stand. All of the mature trees died, whereas only 30–50% of the young trees died while the remainder recovered and resumed growth. The ability to recover from stress, although not understood in specific physiological or pathological terms, was much greater in young trees than in the old ones. The earlier invasion of mature trees by stem insects and fungi appeared to be the result, rather than the cause, of earlier mortality.

Mortality and subsequent deterioration were greater in the spaced defoliated plots than in the unspaced controls. Again, this cannot be explained in terms of differences in defoliation pressure. The differences in mortality and subsequent deterioration were sufficient to cancel much of the volume gains made by spacing.

There were few differences, from the standpoint of secondary insects and decays, between D trees that survived defoliation and resumed growth without the aid of insecticidal sprays and the P trees that were protected by annual applications of trichlorfon. Dead tops were common in the former group, and there was slightly more sap rot in surviving D trees. Wood wasp damage to the lower bole was intense in all surviving trees. However, wood wasp oviposition holes were healed over by subsequent cambial activity

TABLE 4. Proportion of stem wood volume affected by decays and stains in trees with known defoliation histories and dates of mortality

Treatment and deterioration class*	No. of trees	% of total volume (SD)				
		Sap stain and incipient sap rot	Advanced sap rot	Heart rot	Butt rot	Total decay and stain
Defoliated, spaced						
9	1	0.6	66.8			67.3
10	4	31.8	28.6			60.4
		(11.4)	(28.5)			(17.6)
11	6	43.9	14.3	0.1		58.3
		(13.4)	(14.8)	(0.1)		(20.0)
12	3	49.7	4.9	4.0		58.6
		(3.7)	(7.8)	(6.9)		(8.3)
14	3	28.8	0.1			28.9
		(5.2)	(0.1)			(5.4)
15	4	43.7	0.2	0.2		44.1
		(10.2)	(0.4)	(0.4)		(10.5)
16	15	2.6		0.3		2.9
		(10.2)		(1.0)		(11.2)
Defoliated, unspaced						
12	6	38.3	2.2			40.5
		(7.4)	(3.4)			(9.1)
14	3	26.4	4.0			30.5
		(7.9)	(5.7)			(13.5)
15	1	26.6				26.6
16	28	2.8		0.8		3.6
		(3.6)		(4.0)		(5.0)
Protected, spaced						
16	24	0.5		0.1		0.6
		(1.2)		(0.3)		(1.2)
Protected, unspaced						
16	20	0.4		1.3	0.2	2.2
		(0.6)		(4.3)	(0.6)	(4.5)

*For an explanation of the deterioration classes see Table 3.

and there was no evidence of larval development and completion of the life cycles of these insects. The small pockets of firm light brown decay or stain appear to have been compartmentalized in the manner described by Shigo (1984).

Numerous microorganisms were cultured from the trees sampled in this study. Most were recovered in such low numbers that they were not considered significant in the overall deterioration process. All of the more frequently isolated species except *Tyromyces caesius* have been reported previously in association with balsam fir decay. Their sequence of occurrence, relative to the stages of deterioration were much the same as in previous studies (Basham 1959; Stillwell and Kelly 1964) and were similar in the three stand types. The relatively early invasion by *Amylostereum chailletii* has already been discussed with respect to mortality in surrounding stands and a buildup of wood wasp populations.

The stem insects detected in this study were the same species or genera found in other studies of balsam fir deterioration (Basham 1980; Belyea 1952). There was more evidence of weevil (*Pissodes dubius*) activity than reported in previous investigations. There was no evidence of an association of any of the insects, other than the wood wasps, with any particular fungus or defect.

In conclusion, the young balsam fir trees that had been spaced to increase growth rates deteriorated rapidly after death caused by defoliation by the spruce budworm. The initial stages of deterioration were caused by *Amylostereum chailletii* which was established prior to tree death through the activities of wood wasps. Later, other insects, namely ambrosia beetles, bark beetles, sawyer beetles, and weevils attacked the stems and advanced sap rot caused by *Hirschioporus abietinus* developed. Stem deterioration was a consequence of defoliation and mortality and none of the secondary stem invaders were suspected to be direct causes of tree death.

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TABLE 5. Microorganisms isolated on malt agar from decays and stains in balsam fir, all treatments, Crowdis Mountain, Cape Breton Highlands, Nova Scotia

	No. of cultures*				
	Sap stain or incipient sap rots	Advanced sap rot	Heart rots	Butt rots	Dead tops
Basidiomycetes					
Amylostereum chailletii	204	4	4	1	
Coniophora puteana	6			8	
Hirschioporus abietinus	22	26	1		
Perenniporia subacida	2			6	
Resinicium bicolor	2	3		1	
Sistotrema brinkmannii (Bres.) J. Erikss.	6	1			
Stereum sanguinolentum	39	2	33	1	
Tyromyces caesius	30	4			
Other†	31	19	11	3	
Fungi Imperfecti					
Cytospora sp.	33	7			
Pesotum piceae	63	26			
Verticillium sp.	35	5			
Other†	229	56	17	18	6
Bacteria	136	5	3	8	1
Sterile	105	2	7	13	11

*More than one culture sometimes obtained per isolation attempt.
†Includes unidentified, contaminated cultures, and miscellaneous species.

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AXELSSON, R., and ROUTLEDGE, H. 1970. Cleaning young softwood stands: academic exercise or practical solution? Pulp Pap. Mag. Can. **71**: 93–97.

BASHAM, J.T. 1959. Studies in forest pathology. XX. Investigations of the pathological deterioration in killed balsam fir. Can. J. Bot. **37**: 291–326.

_____ 1984. Degradation and loss of wood fibre in spruce budworm killed timber, and effects on utilization. For. Chron. **60**: 10–14.

_____ 1986. Biological factors influencing stem deterioration rates and salvage planning in balsam fir killed after defoliation by spruce budworm. Can. J. For. Res. **16**: 1217–1229.

BASHAM, J.T., and BELYEA, R.M. 1960. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part III. The deterioration of dead trees. For. Sci. **6**: 78–96.

BASHAM, J.T., HUDAK, J., LACHANCE, D., MAGASI, L.P., and STILLWELL, M.A. 1976. Balsam fir death and deterioration in eastern Canada following girdling. Can. J. For. Res. **6**: 406–414.

BASHAM, J.T., MOOK, P.V., and DAVIDSON, A.G. 1953. New information concerning balsam fir decays in eastern North America. Can. J. Bot. **31**: 334–360.

BELYEA, R.M. 1952. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part II. An assessment of the role of associated insect species in the death of severely weakened trees. J. For. **50**: 729–738.

BRANCH, S. 1981. Cape Breton budworm salvage program—a race against time. Can. Pulp Pap. Ind. **34**(4): 45–49.

GIBSON, I.A.S. 1974. Impact and control of Dothistroma blight of pines. Eur. J. For. Pathol. **4**: 89–100.

LOUCKS, O.L. 1959–1960. A forest classification for the Maritime Provinces. Proc. N.S. Inst. Sci. 25(2): 85–165.

MACLEAN, D.A. 1979. Spruce budworm caused balsam fir mortality on the Cape Breton Highlands, 1974–1978. Can. For. Serv. Inf. Rep. M-X-97.

MAGASI, L.P. 1978. Condition of the fir–spruce forests on Cape Breton Island five years after the onset of the current spruce budworm outbreak Can. For. Serv. Inf. Rep. M-X-95.

OSTAFF, D. 1982. Condition of balsam fir on research plots on Cape Breton Island ten years after the start of a spruce budworm outbreak. Can. For. Serv. Marit. For. Res. Cent. Tech. Note No. 65.

_____ 1983. A wood quality study of dead and dying balsam fir — the incidence of Armillaria root rot. Can. For. Serv. Marit. For. Res. Cent. Tech. Note No. 82.

PIENE, H. 1980. Effects of insect defoliation on growth and foliar nutrients of balsam fir. For. Sci. **26**: 665–673.

_____ 1981. Early growth responses to operational spacing in young balsam fir stands on the Cape Breton Highlands. Can. For. Serv. Inf. Rep. M-X-125.

PIENE, H., MACLEAN, D.A., and WALL, R.E. 1981. Effects of spruce budworm caused defoliation on the growth of balsam fir: experimental design and methodology. Can. For. Serv. Inf. Rep. M-X-128.

POWERS, H.R., Jr., MCCLURE, J.P., KNIGHT, H.A., and DUTROW, G.F. 1974. Incidence and financial impact of fusiform rust in the south. J. For. **72**: 398–401.

REED, F.L.C., and ASSOCIATES, LTD. 1978. Forest Management in Canada. Vol. 1. Can. For. Serv. For. Manage. Inst. Inf. Rep. FMR-X-102.

SHIGO, A.L. 1984. Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. Annu. Rev. Phytopathol. **22**: 189–214.

SHORTLE, W.C., and OSTROFSKY, A. 1983. Decay susceptibility of wood in defoliated fir trees related to changing physical,

chemical, and biological properties. Eur. J. For. Pathol. **13**: 1–11.

STALPERS, J.A. 1978. Identification of wood-inhabiting Aphyllophorales in pure culture. Stud. Mycol. No. 16.

STERNER, T.E., EMBREE, D.G., and VAN RAALTE, G.D. 1977. Condition of balsam fir on Cape Breton Island following four years of uncontrolled spruce budworm infestation. Can. For. Serv. Inf. Rep. M-X-80.

STILLWELL, M.A. 1960. Decay associated with woodwasps in balsam fir weakened by insect attack. For. Sci. **6**: 225–231.

_____ 1966. Woodwasps (Siricidae) in conifers and the associated fungus, *Stereum chailletii* in eastern Canada. For. Sci. **12**: 121–128.

STILLWELL, M.A., and KELLY, D.J. 1964. Fungus deterioration of balsam fir killed by spruce budworm in northwestern New Brunswick. For. Chron. **40**: 482–487.

WHITNEY, R.D., HUNT, R.S., and MUNRO, J.A. 1983. Impact and control of forest diseases in Canada. For. Chron. **59**: 223–228.