

Spatial and temporal patterns of balsam fir mortality in spaced and unspaced stands caused by spruce budworm defoliation

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Abstract: Spatial and temporal patterns of balsam fir (*Abies balsamea* (L.) Mill.) mortality were studied during a spruce budworm (*Choristoneura fumiferana* Clem.) outbreak from 1976 to 1984 on Cape Breton Island, Nova Scotia. Natural mortality in four insecticide-protected plots was 0% in spaced and 9–15% in unspaced stands, with only the smallest trees dying. Budworm-caused mortality (i.e., total minus natural) was 31–49% and 11–32% in spaced and unspaced young fir plots, respectively, but reached 94–100% in severely defoliated spaced plots, unprecedented in the literature for young fir mortality caused by the spruce budworm. Mortality began in the fourth to sixth year of defoliation, being earliest in the severely defoliated plots. From 80 to 90% of trees that died had >75% cumulative defoliation, and most (64–100%) of the smallest (2 cm DBH) trees died. There was no significant difference in percent mortality between 25 spaced and 13 unspaced plots ($p = 0.434$), although, on average, mortality was 10–22% higher in the spaced plots. About 20–30% more of the intermediate-sized and largest trees were killed in the spaced plots. High spatial plot to plot variability in mortality occurred, which was apparently related to observed differences in the amount of defoliation and especially the incidence of “back-feeding” (damage to noncurrent foliage), as well as to plot size. Because budworm-caused mortality exhibits a distribution that tends to form large “holes” in stands, the degree of between-plot variability is related to plot size, and it is recommended that small plots that may miss these patches of mortality be avoided.

Résumé : La distribution spatiale et temporelle de la mortalité chez le sapin baumier (*Abies balsamea* (L.) Mill.) a été étudiée lors de l'épidémie de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.) de 1976 à 1984 à l'île du Cap-Breton, Nouvelle-Écosse. La mortalité naturelle dans quatre parcelles protégées par un insecticide était de 0% pour les peuplements éclaircis et de 9 à 15% pour les peuplements non éclaircis où seuls les plus petits arbres mouraient. La mortalité due à la tordeuse, c'est-à-dire la mortalité totale moins la mortalité naturelle, atteignait respectivement 31 à 49% et 11 à 32% dans les parcelles éclaircies et non éclaircies de jeunes sapins. Par contre, dans les parcelles éclaircies où la défoliation était sévère, la mortalité a atteint 94 à 100%, un niveau de mortalité due à la tordeuse jamais rapporté dans la littérature pour de jeunes peuplements. La mortalité a débuté après 4 à 6 ans de défoliation, apparaissant plus tôt dans les parcelles sévèrement défoliées. De 80 à 90% des arbres qui sont morts avaient subi plus de 75% de défoliation cumulative et la plupart (64 à 100%) des arbres les plus petits (2 cm au DHP) sont morts. Il n'y avait pas de différence significative entre 25 parcelles éclaircies et 13 parcelles non éclaircies même si, en moyenne, la mortalité était de 10 à 22% plus élevée dans les parcelles éclaircies. Parmi les arbres les plus gros et ceux de dimension moyenne, environ 20 à 30% plus d'arbres furent tués dans les parcelles éclaircies. D'une parcelle à l'autre, la variation spatiale dans la mortalité était élevée. Cela était apparemment dû aux différences observées dans le degré de défoliation, particulièrement dans l'intensité des dommages sur les aiguilles des années antérieures, et dans la dimension des parcelles. Étant donné que la distribution de la mortalité causée par la tordeuse suit très étroitement celle d'une maladie contagieuse et finit par former des trouées dans les peuplements, le degré de variation entre les parcelles est relié à la dimension des parcelles et on recommande d'éviter les petites parcelles où ces zones de mortalité peuvent être absentes.

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Introduction

Spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks are a recurrent natural disturbance in spruce (*Picea* sp.) and balsam fir (*Abies balsamea* (L.) Mill.) forests in eastern North America. Severe outbreaks have occurred in the 20th century beginning about 1910, 1940, and 1970 (Blais 1983; Kettela 1983; Hardy et al. 1986). Budworm outbreaks cause more uncertainty about spruce–fir stand development and timber yield in New Brunswick than any other factor (Wang 1986; MacLean 1990). An understanding of insect impacts and the effects of outbreaks on stand development must underpin stand growth models and pest management decision–support systems.

Relatively few data exist for patterns of tree mortality in immature stands during spruce budworm outbreaks. Immature fir stands have generally suffered less mortality than mature stands, with averages of 42 and 85%, respectively, for 26 immature and 63 mature plots from several studies (MacLean 1980). Mortality in immature fir stands has been variable, with 40% of the plots analyzed by MacLean (1980) sustaining 21–40% mortality, 15–20% of plots in each of 0–20, 41–60, and 61–80% mortality classes, and 4% in an 81–100% mortality class. Similarly, Baskerville and MacLean (1979) found that budworm-caused mortality in 10 plots in a 35-year-old fir stand ranged from 34 to 84%, with an average of 64%. In some cases, immature fir mortality has been almost as severe as that in mature stands (e.g., Blais 1981).

Two specific questions are addressed in this paper. (1) Do patterns of fir mortality differ between spaced and unspaced stands? No data exist directly comparing mortality in spaced and unspaced stands, and effects on defoliation have been conflicting. Piene (1989a) found higher defoliation in spaced balsam fir stands, but only when budworm population levels were extremely high; Roberts and Chow (1977) measured higher defoliation in semimature, fertilized and thinned black spruce (*Picea mariana* (Mill.) B.S.P.) than in untreated stands; but thinned balsam fir in Quebec did not sustain higher defoliation (Crook et al. 1979), and thinned stands in Minnesota were less defoliated than untreated stands (Batzer 1967). (2) How much spatial variability in mortality occurs? One previous study indicated that mortality in immature stands can be highly variable spatially. Analyzing mortality in 10 randomly located 0.04-ha plots within a homogeneous 8-ha stand, Baskerville and MacLean (1979) found that the extremes of greatest and least mortality occurred within 50 m of one another, and that this was not related to stand characteristics. Also, sequential mortality tended to occur in distinct areas spreading over time, forming a strong patchy distribution, so that variation was a function of the extent to which such patches occurred in each plot. This has important implications for defining stand vulnerability to spruce budworm attack. If within-stand variability in mortality is high and not related to stand characteristics, extensive conventional plot sampling and analysis could lead to statistically significant but artificial relationships between average stand mortality and average stand conditions that are not actually functionally related to the patch mortality (Baskerville and MacLean 1979).

In this paper, we describe the temporal and spatial patterns of mortality in immature balsam fir stands that resulted from a severe, uncontrolled spruce budworm outbreak, and determine their relation to spacing status and tree and stand characteristics. This is one of a series of papers presenting and analyzing results from a detailed study of the development of immature fir stands during a spruce budworm outbreak on Cape Breton Island, Nova Scotia, which occurred from 1976 to 1984 (Piene 1989a, 1989b; Piene and Little 1990; Fleming and Piene 1992a, 1992b).

Materials and methods

Data from three studies were analyzed in this paper: (1) four 0.05-ha spaced and four 0.025-ha unspaced plots measured from 1976 to 1984, with pairs of control (protected by intensive, ground-applied insecticide spraying) and defoliated plots; (2) five 0.05-ha plots measured from 1979 to 1985 in an adjacent area that suffered exceptionally severe defoliation, including “back-feeding” on noncurrent age-classes of foliage; and (3) 63 variable-radius (basal area factor 2.3 m²/ha) plots located systematically over a 1.2 × 0.6 km area that included areas from studies 1 and 2 and established following completion of the outbreak in 1985.

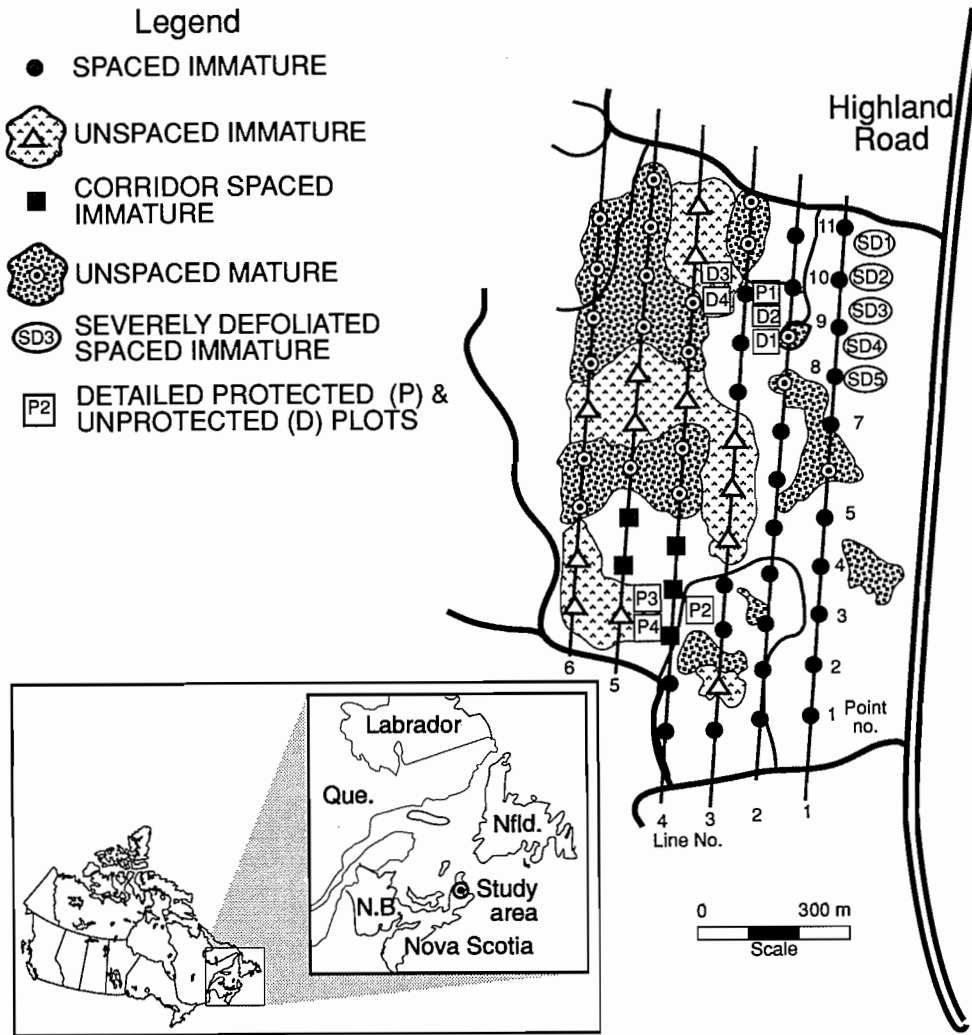
Study 1: Protected and unprotected plots

A description of the study area and procedures used in establishment and measurement of these plots was given by Piene et al. (1981) and Piene (1989a). Young balsam fir stands, which originated following clear-cutting about 1953–1955, were operationally spaced (to 2.4 × 2.4 m, or 8 × 8 ft) in 1971. The budworm outbreak began in 1976, when the stands were 21–23 years old, and consisted of 6 years of severe and 1 year of moderate defoliation (Piene 1989a). Eight plots were established, with one-half sprayed with insecticide each year to serve as controls: spaced protected (P1 and P2) and spaced defoliated (D1 and D2) plots were 0.05 ha and unspaced protected (P3 and P4) and unspaced defoliated plots (D3 and D4) were 0.025 ha (Fig. 1). Each tree in the plots was numbered and measured for standard mensurational characteristics, and locations were mapped. Each tree was assessed annually using binoculars for current-year defoliation and cumulative defoliation (all age-classes of foliage), in percent classes, and was checked annually for mortality. Current defoliation classes were 0–10, 11–20, 21–40, 41–60, 61–80, 81–99, and 100%, and cumulative defoliation classes were 0, 1–10, 11–25, 26–50, 51–75, 76–90, 91–100%; class midpoints were used for calculations.

In all mortality assessments in this paper, trees were only rated as dead after bark was removed from three locations around the stem and examination of the cambium showed discoloration and dryness. Sample sizes were 295 trees from defoliated spaced plots, 605 trees from defoliated unspaced plots, 173 trees from protected spaced plots, and 742 trees from protected unspaced plots.

Defoliation in the protected plots was about 85% of current-year foliage in 1976 (because protection with insecticide only began in 1977) and usually less than 10% of current-year foliage in other years (Piene 1989a). Therefore, any mortality in the protected plots P1–P4 was attributed

Fig. 1. Map showing the location of the study area, 13 permanent plots, and 63 temporary sample plots in immature and mature balsam fir forest on Cape Breton Island, Nova Scotia. Cruise lines ran parallel to the Highland Road, with line 1 being 200 m away; lines and sample plots were 100 m apart.



to natural causes and not to defoliation. Budworm-caused mortality was calculated as total mortality in the defoliated plots minus the natural mortality in the protected plots. Based on their stand densities (Table 1), D3 was paired with P4 and D4 was paired with P3.

Study 2: Severely defoliated plots

In 1977 and 1978, budworm populations on Cape Breton Island were extremely dense, with 10 to 20 times the number normally classed as extreme (Dorais and Kettela 1982) present in both mature (Ostaff and MacLean 1989) and immature (Piene 1989a) stands. In the study area, this resulted in complete destruction of the current-year foliage in both years, as well as severe back-feeding on needles of older age-classes. Cumulative defoliation during 1977–1978 consisted of complete removal of 4.4 age-classes of foliage in unspaced plots D3 and D4, and 5.3 age-classes of foliage in spaced plots D1 and D2 (Piene 1989a). This level of feeding was unprecedented in immature

balsam fir stands, and led us to establish five additional 0.05-ha circular plots in spaced stands (SD1–SD5 in Fig. 1) in this severely defoliated stratum of the study area, to evaluate the resulting mortality. These plots were located in a line 50 m apart. Tree and defoliation measurements were as in study 1. A total of 421 trees were sampled each year from 1979 to 1985, with numbers of trees in the five plots ranging from 54 to 114.

Study 3: Forest cruise line plots

In 1985, following collapse of the budworm outbreak, 63 variable-radius (basal area factor 2.3 m²/ha) plots were measured in a systematic 100 × 100 m grid over a 1.2 × 0.6 km area that included the areas with plots used in studies 1 and 2. These were temporary plots that were only measured once. The area included four stand types, and each plot was categorized as one of spaced immature (25 plots), unspaced immature (13), unspaced mature (20), or corridor spaced immature (5) (Fig. 1). The corridor

Table 1. Summary of stand characteristics of the Cape Breton mortality plots.

Plot type	Plot No.	Density (stems/ha)	Basal area (m ² /ha)	Total vol. (m ³ /ha)*	Mean DBH (cm)*	Mean height (m)*
Detailed protected and unprotected plots						
Protected spaced	P1	2 180	14.2	41.7	8.8	5.0
	P2	1 760	14.6	46.7	9.9	5.6
Protected unspaced	P3	10 480	44.1	145.9	7.0	5.7
	P4	20 640	46.1	129.6	4.9	4.4
Defoliated spaced	D1	2 780	17.1	46.6	8.5	4.8
	D2	3 060	14.4	36.4	7.3	4.1
Defoliated unspaced	D3	13 120	48.0	135.7	6.6	5.0
	D4	11 560	44.9	131.1	6.8	4.9
Severely defoliated plots						
Defoliated spaced	SD1	1 080	12.0	43.1	11.4	6.2
	SD2	1 320	13.5	48.0	11.1	6.2
	SD3	1 940	15.4	50.2	9.6	5.5
	SD4	1 780	21.5	83.7	11.3	6.3
	SD5	2 280	19.4	63.0	10.0	5.6
Forest cruise-line defoliated plots						
Spaced immature	25 plots	3 180	16.6	—	6.7	—
Unspaced immature	13 plots	11 910	41.9	—	5.5	—
Unspaced mature	20 plots	5 370	40.6	—	8.3	—
Corridor spaced imm.	5 plots	18 570	25.8	—	3.6	—

Note: —, not determined.

*For trees with diameter at breast height ≥ 2 cm.

spaced immature stands had been machine cut in 1971, with 3 m wide strips where all trees were removed alternating with 4 m wide uncut strips (Piene 1981). Each tree in the prism sweep was recorded by species, diameter at breast height (DBH), and whether alive or dead, and per plot and per hectare values were calculated. This sample consisted of 829 trees, or an average of 13 trees per sample plot. Data from the unspaced mature plots were included in the analysis to allow comparison with the immature plot mortality in the same area.

Results and discussion

Description of the sample plots

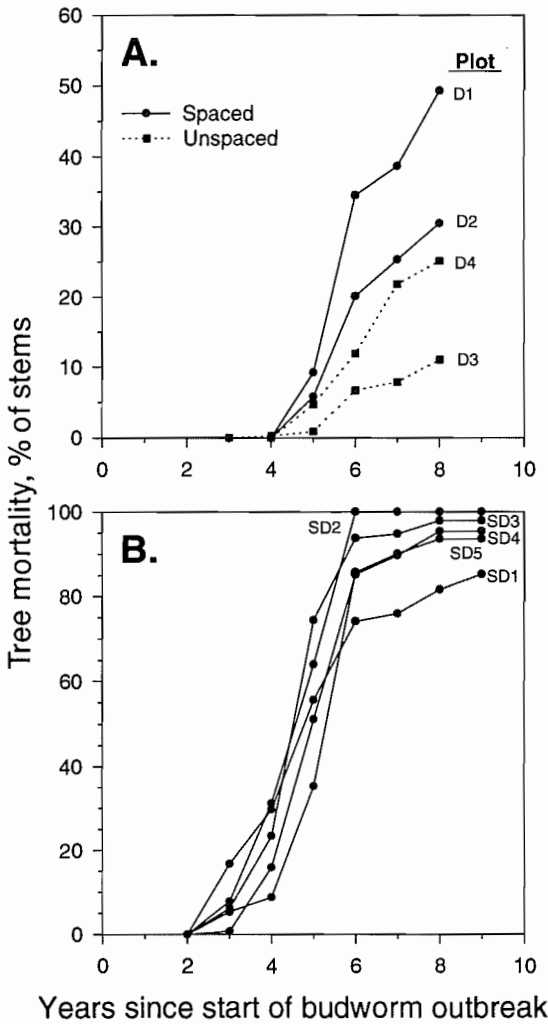
Spaced plots examined in this study ranged in density from 1080 to 3180 stems/ha, while unspaced plots were considerably denser at 10 480 to 20 640 stems/ha (Table 1). The corridor (machine) spaced plots averaged 18 570 stems/ha. The relatively high density of the mature plots sampled in the forest cruise lines, at 5370 stems/ha, probably reflects inclusion of some unspaced immature trees in the prism sweeps; i.e., the plot locations were selected at predetermined distance intervals and categorized as one of the four plot types, rather than being chosen to be representative of particular types. As would be expected, basal area of the unspaced immature plots, at 42–48 m²/ha, was two to three times as high as that in the spaced plots. Other characteristics of the study plots are summarized in Table 1.

Temporal patterns of mortality

Defoliation in the protected plots was about 85% of the current-year foliage in 1976 only, and usually less than 10% of the current-year foliage each year from 1977 to 1984 (Piene 1989a). No trees died in the insecticide-protected spaced plots P1–P2, and the 9–15% mortality observed in the protected unspaced plots P3–P4 was all in small, suppressed trees less than 6 cm DBH. This was natural, competition-induced mortality and was not caused by the spruce budworm.

Budworm-caused tree mortality began in 1980 (the fifth year of defoliation) in the defoliated plots D1–D4 and in 1979 (the fourth year) in the severely defoliated plots SD1–SD5 (Fig. 2). Mortality tended to occur somewhat earlier in the spaced than in the unspaced stands. Mortality in immature fir stands has generally begun in the fifth to seventh year of the outbreak (MacLean 1980). Total budworm-caused mortality reached, respectively, 49 and 31% in the spaced plots D1 and D2, 11 and 24% in unspaced plots D3 and D4 (actually, total mortality was 26 and 35% for D3 and D4, but the 9–15% natural mortality from P3–P4 was subtracted from this), and 94–100% in the spaced severely defoliated plots SD1–SD5. With the exception of SD1–SD5, these levels of mortality were similar to the range of 30–70% in immature fir stands reported by MacLean (1980) for several studies, or the 40% volume loss found by Solomon and Brann (1992) for immature stands (mean diameter class 4.6–6.5 in., or

Fig. 2. Temporal patterns of young balsam fir mortality in (A) defoliated spaced and unspaced plots and (B) severely defoliated spaced plots. The first year of defoliation (year 0) was 1976.

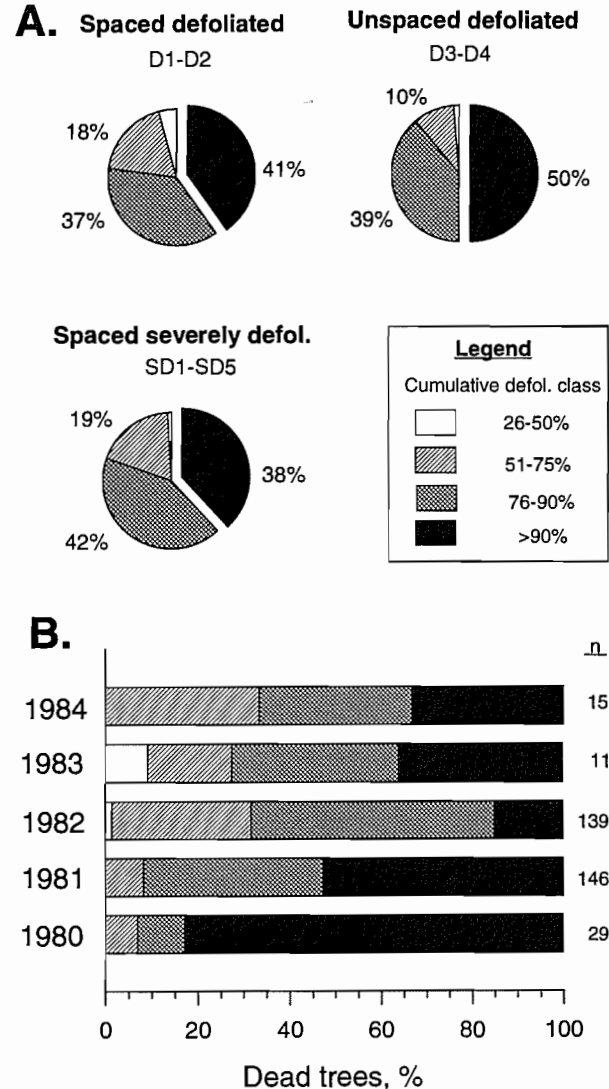


11.7–16.5 cm). The mortality in SD1–SD5 was unprecedented in the literature for young fir stands, in terms of occurring exceptionally early in the outbreak, increasing extremely rapidly (50–80% of the stand dying in a 3-year period), and reaching such high ultimate mortality levels (Fig. 2). This undoubtedly reflects the heavy defoliation (including back-feeding) of four to five complete age-classes of foliage that occurred in the vicinity of these plots in 1977–1978 (Piene 1989a).

Which trees die? Mortality by defoliation and size class

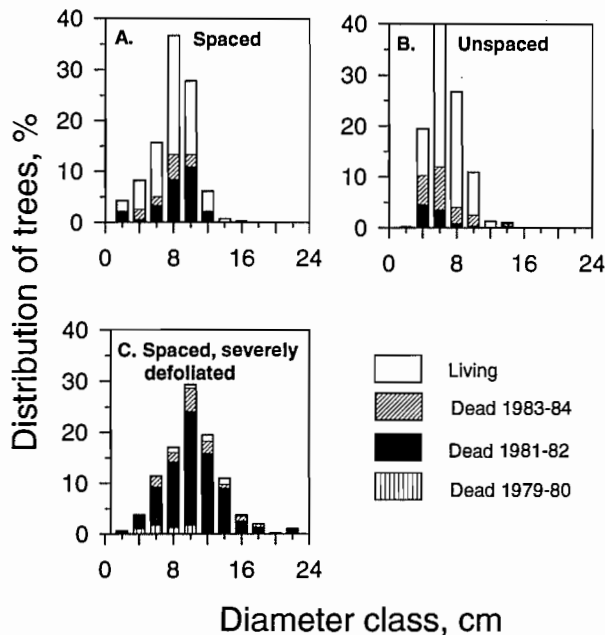
Distribution of dead trees by amount of cumulative defoliation (all age-classes of foliage) in the previous year is presented in Fig. 3A. Overall throughout the outbreak, 38–50% of trees that died in the following year had >90% defoliation, and 78–89% had >75% cumulative defoliation. Distribution of dead trees by the previous year's defoliation class was very similar for spaced plots D1–D2 and SD1–SD5, whereas in the unspaced plots D3–D4, more

Fig. 3. Distribution of dead trees by cumulative defoliation class in the previous year. (A) All dead trees in 1980–1984 for spaced defoliated plots D1–D2 ($n = 92$), unspaced defoliated plots D3–D4 ($n = 144$), and spaced severely defoliated plots SD1–SD5 ($n = 343$). (B) Dead trees each year from 1980 to 1984 for plots SD1–SD5.



of the trees that died were in the most severely defoliated class (Fig. 3A). Figure 3B shows that a higher proportion of trees in the 76–90% and 51–75% defoliation classes died in the following year as the outbreak progressed from 1980 to 1984; 83% of trees that died in 1980 had >90% cumulative defoliation, but by 1983–1984, only about 35% of the dead trees had been in the most severely defoliated class. However, it is important to note that most mortality occurred before 1983 and only 26 trees died in 1983–1984 (Fig. 3B), so sample sizes at the end of the outbreak were small. More trees dying in less-heavily defoliated classes might be thought to reflect increased importance of diseases such as *Armillaria* root rot (found in mature stands by Ostaff 1983) as trees become weakened, but Wall (1988) showed for plots D1–D4 that secondary insects and disease stem invaders were not direct causes of tree death, and

Fig. 4. Distribution of surviving balsam fir, and trees that died in 1979–1980, 1981–1982, and 1983–1984, by diameter class, for (A) spaced plots D1–D2, (B) unspaced plots D3–D4, and (C) spaced severely defoliated plots SD1–SD5.

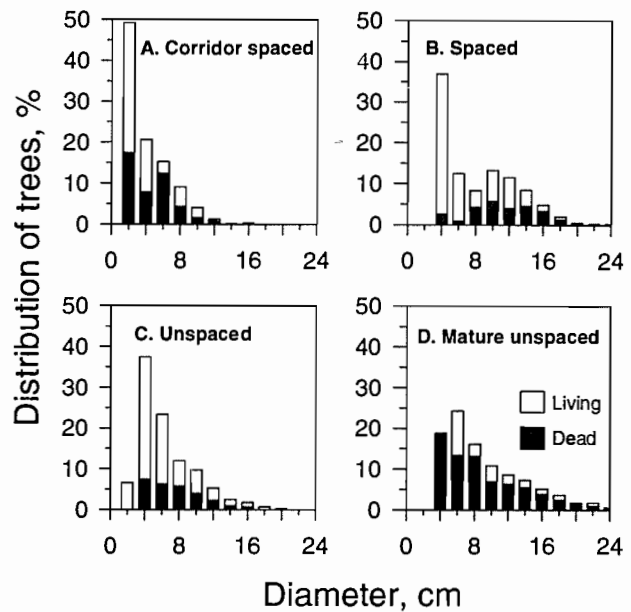


examination of several root systems in D1–D4 did not show *Armillaria*. Nevertheless, these data definitely show more trees dying with cumulative defoliation less than 90% than was observed for mature balsam fir stands on Cape Breton Island (MacLean and Ostaff 1989).

Frequency distributions of living and dead trees by plot type, DBH class, and 2-year time of death periods are shown in Fig. 4. The overall diameter distributions clearly reflect the effect of the spacing treatments in 1971; i.e., a higher proportion of smaller trees in the unspaced plots. Only the spaced severely defoliated plots SD1–SD5 suffered any mortality during 1979–1980, and this was entirely among trees <10 cm DBH. The subsequent heavy mortality in SD1–SD5 affected all DBH classes equally (Fig. 4C). There were differences between D1–D2 and D3–D4, however, with a higher proportion of intermediate-sized trees dying in the spaced plots; this may partly reflect the spacing treatment resulting in more of these larger trees. In the spaced D1–D2 and unspaced D3–D4 plots, respectively, 64 and 100% of 2 cm DBH trees died, 32–37 and 15–53% of 4–8 cm, 48 and 24% of 10 cm, 38 and 15% of 12 cm, and no >14 cm trees died (Figs. 4A, 4B).

Frequency distributions of living and dead trees were quite different among spaced, unspaced, and mature cruise-line plots (Fig. 5). In the mature plots, all 4 cm DBH trees, 60% of 6 cm, and about 70–80% of all larger trees died (Fig. 5D). This was similar to the 73–86% mortality in each 5 cm DBH class found for other mature balsam fir plots on Cape Breton (MacLean and Ostaff 1989). In the spaced plots, only 10% of trees <6 cm died, along with 40–50% of 8–14 cm and 70–80% of trees >14 cm (Fig. 5B). In the unspaced plots, 20–30% of 4–6 cm trees

Fig. 5. Distribution of living and dead balsam fir, by diameter class, at the end of the outbreak for (A) corridor spaced immature ($n = 56$), (B) spaced immature ($n = 184$), (C) unspaced immature ($n = 236$), and (D) unspaced mature ($n = 353$) trees.



and generally 40–50% of trees >6 cm died (Fig. 5C). Overall, two trends were evident: few of the smallest trees <8 cm DBH died in either the spaced or unspaced young fir plots; and about 30% more of the largest trees >14 cm DBH died in the spaced than in the unspaced plots.

Clearly, exceptionally severe defoliation will override any other causal relationships between amount of mortality and tree characteristics. This appears to have occurred in plots SD1–SD5, with uniformly heavy mortality across all DBH classes, as was previously observed for mature fir (Blais 1981; MacLean and Ostaff 1989). In both spaced D1–D2 and unspaced D3–D4 plots, over one-half of the small suppressed trees died, similar to the findings of most earlier studies (Blais 1958, 1980; Batzer 1973; Baskerville and MacLean 1979; Lawrence and Houseweart 1981; MacLean et al. 1984). Blais (1958) and Baskerville and MacLean (1979) found that suppressed and intermediate trees died first and hypothesized that this was because larvae dropping from larger crowns land on trees in the lower crown classes in sufficient numbers to kill these weaker trees. Kleinschmidt et al. (1980) was the only study to observe a higher defoliation intensity on the smaller fir trees.

When trees sustain comparable defoliation levels, whether they survive or die may be governed by their ability to refoliate after feeding. Piene (1989a) concluded, based on 7 trees that survived the outbreak and 10 trees that died, that the recovery of balsam fir after defoliation is more attributable to an ability to produce buds than to differential feeding. Piene suggested that differential host response (i.e., why one tree lives and another dies) results from an ability to produce epicormic shoots and may be partly genetically controlled.

Table 2. Mean and distribution of balsam fir mortality, caused by spruce budworm, in four types of plots across a 1.2 × 0.6 km grid sampled following completion of the outbreak.

Plot type	n	Mortality, % basal area		% of plots by 20% mortality class				
		Mean	SE	0-20	21-40	41-60	61-80	81-100
Spaced immature	25	42.4	7.8	44	4	16	12	24
Corridor spaced immature	5	56.2	14.5	20	20	0	40	20
Unspaced immature	13	32.4	9.2	46	15	24	0	15
Unspaced mature	20	69.0	5.8	5	10	15	35	35

Note: Student's *t*-test showed that mean mortality in unspaced mature plots was greater than that in spaced immature ($p = 0.012$) or unspaced immature ($p = 0.001$) plots, but all other comparisons were not significant ($p > 0.05$).

Mortality in spaced versus unspaced plots

So, did more trees die in the studied spaced than in unspaced plots? On the basis of our results, the answer is no. Although mean mortality was 22% higher in spaced D1-D2 than in unspaced D3-D4 plots (Fig. 2A) and 10% higher in spaced than in unspaced cruise-line plots (Table 2), statistically, there was no significant difference (for the cruise-line plots, $p = 0.434$, Student's *t*-test, $n = 25$ spaced and 13 unspaced). In fact, the most striking aspect of mortality in these young fir stands was the wide variability among the cruise-line plots. Mortality in both spaced and unspaced line plots ranged from 0 to 100%, and distributions of the plots among 20% mortality classes were roughly similar (Table 2). Comparing spaced and unspaced plots, respectively, 44-46% had 0-20% mortality, 4-15% had 21-40% mortality, 16-24% had 41-60% mortality, 0-12% had 61-80% mortality, and 15-24% had 81-100% mortality. Mortality in the corridor spaced plots averaged 56% (Table 2), and ranged widely from 17 to 100%. Similar wide variability in mortality in young fir stands was also shown by MacLean (1980). As has been shown in numerous other studies, mature plots more consistently suffered heavy mortality, with a mean of 69% (Table 2), and 70% of the mature plots had >60% mortality. The mature plots had significantly higher mortality than the young spaced ($p = 0.012$) and unspaced ($p = 0.001$) plots.

As would be expected, the severely defoliated SD1-SD5 plots had significantly higher mortality than both the defoliated spaced D1-D2 ($p = 0.0004$) and unspaced D3-D4 ($p = 0.0004$) plots. Thus, severe defoliation will override any possible differences between spaced and unspaced plots.

Spatial patterns of mortality

Is there a spatial dimension to the wide variability in mortality within a particular type of plots? The data from the cruise-line plots clearly showed that there is. The higher basal area mature and unspaced plots tended to be towards the right and back of the geographic sample grid, as depicted in Fig. 6A. The five corridor spaced plots were all located adjacent to one another. In general terms, those spaced plots that had high (>60%) mortality were located either in the severely defoliated area near plots SD1-SD5

(Fig. 1) or adjacent to the predominantly mature forest (Fig. 6B). Most of the low-mortality spaced plots were also located in one particular area, toward the front and left of Fig. 6B. However, as noted by Baskerville and MacLean (1979), extremes of mortality can occur immediately adjacent to one another, with 93% mortality in spaced plot line 1, point 1 versus 0% mortality for point 2 on the same line.

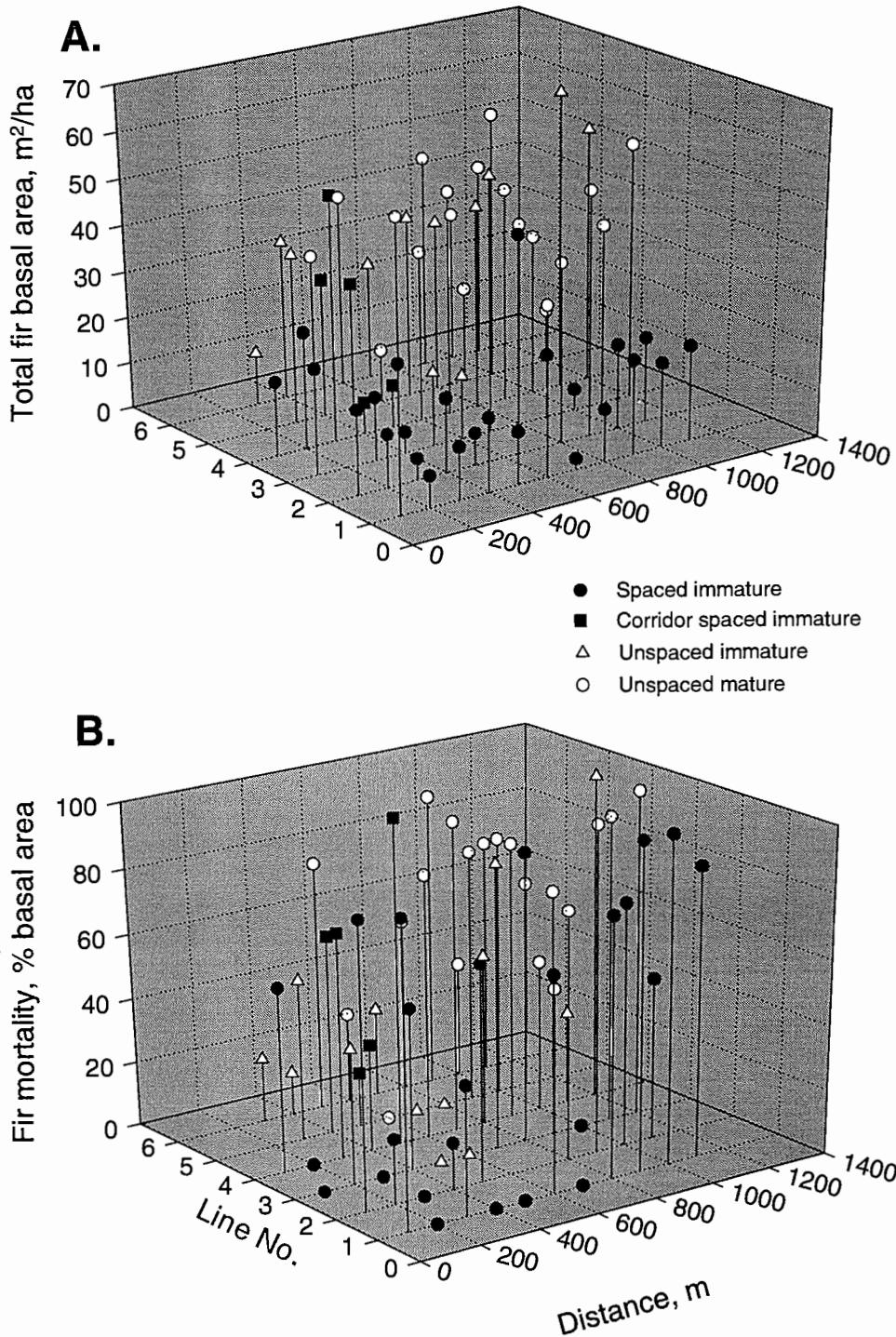
The four unspaced plots and one mature plot that sustained no mortality were all located within 200 m of one another on lines 3 and 5 (Fig. 6B). However, in between these plots on line 4 was a mature plot that sustained 81% mortality.

Only two studies have previously documented spatial patterns of tree mortality and plot to plot variability caused by budworm outbreaks. Baskerville and MacLean (1979) determined that the extremes of budworm-caused mortality occurred within 50 m of one another, and that this was not related to stand characteristics. The authors concluded that variation was likely caused by differences in budworm pressure from plot to plot, as might result from uneven within-stand moth dispersal, that were unrelated to stand characteristics. Baskerville and MacLean (1979) also showed that within plots, there were striking patterns of mortality, with sequential mortality tending towards a distribution that resulted in "holes" in the stand as mortality progressed. The variation in mortality from plot to plot was thus related to the extent to which such "mortality patches" occurred in each plot.

In the second study, on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) mortality caused by western spruce budworm (*Choristoneura occidentalis* (Freeman)), plot to plot variability in total mortality was also high (Alfaro et al. 1984). About 30% of the 114 plots had mortality levels in the 0, 1-25, and 26-50% basal area mortality classes, while 9 and 3% had 51-75 and >75% mortality, respectively. Most mortality occurred among small, suppressed, and intermediate trees, and Alfaro et al. (1984) concluded that the random spatial distribution of these small trees throughout the stand might explain the highly variable pattern of mortality in the stand.

The data collected for these cruise-line plots do not

Fig. 6. Total balsam fir basal area (A) and fir mortality (B) for 63 plots located at 100-m intervals across a 1.2 × 0.6 km grid on Cape Breton Island. Plots were categorized as spaced immature, corridor (machine) spaced immature, unspaced immature, and unspaced mature.



allow determination of why the differences in mortality occur. However, it is likely largely due to differences in the amount of defoliation, reflecting patchiness of degree of attack by the spruce budworm. Detailed sampling within the spaced D1–D2 and unspaced D3–D4 plots showed that defoliation was uniform among trees in these plots

(Piene 1989a). The spaced plots that sustained heavy mortality (Fig. 6B) were all located in one area, near the severely defoliated permanent plots SD1–SD5 (Fig. 1), and it is clear that the severe mortality there was attributable to extremely high budworm populations that resulted in heavy back-feeding.

There are significant sampling implications of the spatial variability in mortality (and probably defoliation) observed in this study. Clearly, between-plot variability far exceeds variability in defoliation or mortality between shoots within a branch, branches within a tree, or trees within a plot (MacLean and Lidstone 1982; MacLean and Ostaff 1983; MacLean 1984). Further, because of the patchy pattern of mortality, plot size strongly influences the range of mortality in the data (Baskerville and MacLean 1979). This would explain the wider variation in mortality in the small cruise-line variable-radius plots (average 13 trees/plot) than in the 0.05-ha plots D1–D2 and SD1–SD5 (range 54–153 trees/plot). It would also suggest that small plots should be avoided in surveys of budworm-caused mortality.

Net effects of the spruce budworm outbreak on spaced and unspaced stands

Overall, the spruce budworm outbreak was more damaging for spaced than for unspaced stands. The spacing treatment represented a significant (in excess of \$700/ha) investment that is designed to produce optimum spatial growing conditions. This results in substantial increases in growth rate (45–60 and 77–136%, respectively, for low- and high-density stands: Piene 1981) and shortened rotation lengths (Piene 1982); however, every tree in the stand following the spacing is expected to be a crop tree. The budworm outbreak, therefore, killed 31–49% of the crop trees in spaced plots D1–D2, likely resulting in one-third to one-half less volume at the time of harvest (Baskerville and MacLean 1979). The severely defoliated plots SD1–SD5, with 94–100% mortality, were a total loss. These results are probably typical of spruce budworm impact in eastern Canada, with the most heavily damaged area representing the most severely defoliated stratum.

The unspaced stands D3–D4 also suffered 26–35% total mortality or 11–24% budworm-caused mortality, but given the initial 12 000 – 13 000 stems/ha density, 7800–9600 stems/ha survived the outbreak, so the stands may still be overstocked. The spatial distribution of the surviving stems will be strongly clumped, based on mortality patterns observed in this study and Baskerville and MacLean (1979), and so will be less than optimum for timber production.

The rationale for forest managers to precommercially space softwood stands is that by increasing growth rates and thereby shortening rotation length, sustainable harvest levels can be substantially increased (termed the “allowable cut effect”). Thus, a management strategy that included allowing the spruce budworm to “thin” stands during outbreak periods would result in considerably lower growth rates during outbreak periods, lower stand volumes, and longer rotations than a management policy that included judicious insecticide use to protect trees from defoliation.

In conclusion, the significant results of this study can be summed up as follows: (1) natural mortality in immature plots very well protected with insecticide was 0% in spaced and 9–15% (the smallest trees only) in unspaced plots, over an 8-year period; (2) budworm-caused mortality in the same period was 31–49 and 11–32% in spaced and unspaced young fir plots, respectively, but reached 94–100%

in severely defoliated young spaced plots; (3) mortality began in the fourth to sixth year of defoliation, being earliest in the severely defoliated plots; (4) 80–90% of trees that died had >75% cumulative defoliation, and most (64–100%) of the smallest (2 cm DBH) trees died; (5) there was no significant difference in percent mortality between spaced and unspaced plots, although mortality averaged 10–22% higher, and about 20–30% more of the intermediate-sized and largest trees were killed, in spaced plots; and (6) high spatial plot to plot variability in mortality occurred, but this was likely related to observed differences in amount of defoliation, and especially the incidence of back-feeding.

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